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The Genera of Pore Fungi

Wm. Bridge Cooke*

Species of fungi with pores or pore-like structures in which the hymenium is produced have been assigned to about 300 genera which are discussed in this paper. The plan [adopted] is to present the names of these genera in alphabetic order, indicate the species upon which the genera were based or are thought to have been based, and indicate the validity of the use of these genera in connection with species or groups of species.

Approximately 100 of these genera can be considered valid or usable, and some of these can no longer be considered polypores but are more nearly related to such provisional groups as the "Cyphellaceae", "Meruliaceae", "Coniophoraceae", and possibly other groups. Some of these valid genera cannot be used because they are synonymous with others, the extent of the synonymy not determinable until all the species of any group are thoroughly investigated in the light of one or more of the systems of classification to be discussed below, or a synthesis of all these systems.

Many genera are unavailable for use, as indicated by the large number of genera with common type species (obligate synonyms). The erection here of new genera to replace genera considered invalid on any bases is not attempted.

Usage of the genera listed below by current monographers of the polypores will be indicated with each genus involved. Except within schools of taxonomy of the polypores, no two workers have ever agreed completely on the generic limits of the group. As many systems of polypore taxonomy have been in use as schools of workers have existed.

It might be of interest to present some comments on the points of view of workers who have studied the polypores. These comments are based on various publications and monographic treatments. Fries (1821) used only two of the polypore genera, *Daedalea* and *Polyporus*, in addition to *Merulius*, *Boletus*, and *Fistulina*. In the following discussion *Boletus* and its more recent segregates will not be considered. These genera, members of the Agaricales rather than the

*In Charge, Fungus Studies, Robert A. Taft Sanitary Engineering Center, U. S. Department of Health, Education, and Welfare, Bureau of State Services, Public Health Service, Cincinnati 26, Ohio.

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Polyporales, have been treated in recent times by Snell (1942), and by Singer (1947–48 and 1951). *Merulius*, of the Meruliaceae, *Serpula*, of the Coniophoraceae, and *Fistulina*, of the Fistulinaceae, will be mentioned below because for a long time and by most workers they have been assumed to be polypores.

The first worker to add genera to the original two of Fries was S. F. Gray (1821). He proposed nine genera in addition to the three nonpolypore genera used by Fries. Most of these are usable today in the segregation of *Polyporus* and *Daedalea* which are too unwieldly for use as Fries presented them. They are not homogeneous groups of species.

Fries, in subsequent works, added genera and accepted genera of others until in 1874 he recognized eight genera of polypores and seven genera in which the hymenium is produced in pore-like structures but which are not considered among the "true" polypores. Even then he did not recognize *Fomes*, and we have to drop back to 1867 to a rather obscure work by Kickx to find this genus published for the first time together with five other polypore and three nonpolypore genera, all of which had been in use prior to 1867. While *Fomes* is one of the genera attributed to Gillet (1874) he was not the first to use it although it appears among the nine polypore and five nonpolypore genera he accepted. Winter (1884) in Rabenhorst, added nothing to the picture since he held a rather conservative interpretation of the Friesian series. Most of the genera Quélét (1886) used in listing the fungi of France were new; ten of the 15 genera in which he placed the true polypores had not appeared previously in the literature. Most of these were used for various segregate groups of the polymorphic *Polyporus* Fr. In 1889 Schroeter adopted seven genera for the true polypores of a limited area in northern Germany; of these several were new, others were taken from Fries and Karsten. Starting in 1879 P. A. Karsten segregated species originally assigned to *Polyporus* and *Daedalea* together with species based on specimens sent him from many parts of the world. By 1889 Karsten had listed species he assigned to 26 genera. Of these genera, many are considered good today. Karsten's generic diagnoses are very brief in many cases, and it is difficult to tell upon what bases his segregations were made beyond the desire for units with fewer species which are more homogeneous and with which it is easier to work.

M. C. Cooke (1884–5) added little except that he amplified the idea of a generic unit for resupinate species—*Poria*. Saccardo can be mentioned briefly although he was a compiler rather than a monographer. In 1888 he listed species assigned to 13 true polypore genera; by 1925 the Saccardoan compilers had increased this number to 18. Many of the genera introduced prior to 1925 and after 1888 had been reduced to synonymy in the pages of the Sylloge, or were ignored. C. G. Lloyd started publishing his important Mycological Writings in 1898 and by 1925 he had discussed many species in only 12 genera. In spite of the many species he studied, and the many personalities with whom he came in contact, he never accepted most generic segregates and it is doubted if he condoned the raising of his subgeneric units to generic rank. As for his own creations, these were always

made lightly in the name of Prof. N. J. McGinty and will be commented on later.

P. Hennings (1900), in Engler and Prantl, recognized only 11 genera as well as six "excluded" genera of doubtful position. M. C. Cooke had access to material from Europe and throughout the British Empire; Saccardo had access to the world's literature, while C. G. Lloyd received material from all over the world and had access to all the collections in Europe as well as North America. Thus these workers could have attempted to monograph the species of the world and their work could have been definitive. Since their time, and except for Killermann and Clements and Shear of whom the above remark can be made, students of the group have been interested in the species of restricted areas.

Patouillard (1900) was one of the earliest writers to arrange the polypores in what may be considered a modern treatment. He used hymenial configuration as a basic means of separation of the Hymenomycetes. The family *Aphyllophoraceae* (to modernize his spelling) was separated from the other families of the homobasidiomycetous fungi (*Exobasidiaceae*, *Agaricaceae*, and *Gasteromycetes*) by reason of its normal, hemiangiocarpous structure with hymenium capable of being produced indefinitely. He divided the family into two tribes. Of these the *Porohydneae* were further divided into four subtribes among which were included the *Poreae*. This was divided into four groups, two of these were further divided into three series each and a list of artificial genera was appended to the analysis of this subtribe.

In "*Les Polypores Vrais*" Patouillard included the series *Polypores*, *Leucopores* and *Leptopores*. In "*Les Fomes*" he included the series *Trametes*, *Igniaires* and *Placodes*. Neither "*Les Merules*" nor "*Les Fistulines*" were divided into series. A total of 39 genera were listed.

Murrill, 1907 *et seq.*, recognized 74 genera of true polypores. Many of these he originated, many he adopted from earlier workers. He divided the Polyporaceae into 4 subfamilies: *Poriae* for resupinate species; *Polyporeae* for annual, light or dark-colored species which are stipitate or sessile; *Fomiteae* for perennial, light or dark-colored, stipitate or sessile species; and *Daedaleae* for species which are annual or perennial, stipitate or sessile and with the hymenophore not strictly porose but modified to daedaleoid or lenzitoid. Murrill tried to cover the species of North America and parts of South America, using European herbaria as well as his own collections and those of correspondents as guides to concepts of type specimens or species. His basis for segregating genera was in part anatomic, in part morphologic.

Adeline Ames (1913), upon the basis of a series of anatomic studies on a wide range of specimens of most species from eastern North America, recognized 16 genera, in some cases adjusting generic descriptions of earlier genera to fit her findings.

In England, Carlton Rea (1922), following the system of Patouillard, recognized 10 genera for the British Isles. The area covered is restricted and the concepts used are based on anatomic and morphologic characters.

In France, Bourdot and Galzin (1927) also following the Patouillardian system arrived at 17 genera for western Europe. The area is of somewhat larger size and includes a larger variety of habitats so that a

larger number of species was studied on the basis of anatomic and morphologic characters.

In 1931 Clements and Shear published a list of all genera published up to that time and known to these authors. In this list the names of 13 polypore genera appear as recognized by these authors. Killermann, 1928, in Engler and Prantl, recognized 13 good genera, 2 atypical genera, and 7 unplaced genera. Many of these were divided into 2 to 11 subgenera. This appears to be the latest attempt to summarize the polypores of the world.

Among North American treatments are several localized ones several of which should be mentioned: Neuman (1914) recognized eight genera in Wisconsin; Shope (1931) listed species in seven genera from Colorado; Overholts (1933) described species in eight genera from Pennsylvania; and Lowe (1942, 1946) described species in nine genera from New York State. Earlier Overholts had treated the species from Ohio (1913) and from the Middle Western United States (1915) using a similarly limited number of genera (Cooke, 1954).

In 1927, Cunningham in New Zealand listed the polypores as representing five genera in the subfamily *Polyporeae* of the *Polyporaceae*. More recently he has treated the species of New Zealand, and listed the species of Australia (1947–1950), on the basis of the anatomical studies made possible by Corner's (1932) findings (Cunningham, 1947). On these bases he recognized three subfamilies of the *Polyporaceae* including the resupinate species in the *Poriae*, the light color context species with annual or perennial habit in the *Polyporeae*, and the dark color context species with annual or perennial habit in the *Fomitae*. He recognized 12 genera in New Zealand. His studies were not only based on fresh material, but on a review of all material in the Kew Herbarium. As a system of classification based on hyphal systems it leaves much to be desired. As a system of classification of the Polyporaceae it is hardly a start, for it is based solely on a somewhat erroneous interpretation of Corner's original concepts of hyphal systems which were not too clearly stated, and it ignores many characters readily available and considered by many workers to be more fundamental than hyphal types no matter how fixed they may appear to be genetically. This is best demonstrated by a paper in which Cunningham (1954) described his ideas of how hyphal system concepts can be applied in the clarification of concepts of such large genera as *Fomes* and *Polyporus*. He segregated *Fomes* into five genera, three with dimitic hyphal systems, two with trimitic systems. Among those with dimitic systems species with hyaline hyphae would go in *Fomitopsis* based on *Fomes annosus*. Brown hyphal species with smooth spores were placed in *Fomes* based on *F. igniarius*, and those with ganodermatoid spores were placed in *Elfvingia* based on *E. applanata*. In the group with a trimitic hyphal system *Ganoderma* based on *G. lucidum* has hyaline hyphae and ganodermatous spores, while species with brown hyphae and smooth spores were placed in *Elfvingiella* based on *E. fomentaria*. *Polyporus* was divided by following adherence to a system based on hyphal types, pore types, spore types, and basidial types, into the following genera, with species considered typical: *Polyporus* (*P. arcularius*), *Irpex* (*I. lacteus*), *Coriolus* (*C. zonatus*),

Lenzites (*L. betulina*), *Coltricia* (*C. perennis*), *Inonotus* (*I. cuticularis*), *Hapalopilus* (*H. lutescens?*), *Amauroderma* (*A. schomburgkii*), *Trametes* (*T. odorata*), and *Daedalea* (*D. confragosa*).

In 1934, M. A. Donk, working in The Netherlands, developed an entirely different system of classification of the *Aphyllophoraceae*. For this country Donk recognized 29 genera of polypores which he distributed through four subfamilies and five tribes: The *Boletopseae* in the *Phylacteroideae;* the *Polyporeae, Tyromyceteae* and *Daedaleae* in the *Polyporoideae;* the *Ganodermoideae;* and the *Hymenochaetoideae*.

In 1941, Bondartsev and Singer, working in Russia, largely with material from Russia, Siberia, and parts of Europe, placed the 60 polypore genera with which they worked, in six suborders of the *Aphyllophorales*. Seven families, five subfamilies, and 10 tribes were used. These higher categories include: *Phylacteriineae: Boletopsidaceae; Clavariineae: Scutigeraceae; Polyporiineae: Polyporaceae; Cyphelliineae: Fistulinaceae;* and *Corticiineae: Corticiaceae* and *Meruliaceae*. The family *Polyporaceae* was divided into subfamilies as follows: *Poroideae*, including most of the resupinate species, with eight genera; *Tyromycetoideae* with seven genera; *Fomitoideae* with six tribes including the *Piptoporeae* with two genera, *Ischnodermateae* with three genera; *Fomiteae* with two genera, *Phaeoleae* with one genus, *Inonteae* with six genera, and *Ganodermateae* with one genus; *Polyporoideae* with two genera; and the *Corioloideae* with the four tribes: *Corioleae* with 14 genera, *Oxyporeae* with six genera, *Hirschioporeae* with one genus, and *Daedaleae* with four genera.

Between 1936 and 1942 Pilát, in Czechoslovakia, working largely with European material, but also studying specimens sent by correspondents in the United States and Siberia, published an extended treatise on the polypores in which he recognized 23 genera. These were placed in the *Polyporaceae* (with *Fistulina* in the *Fistulinaceae*) which was divided into three subfamilies: *Ganodermoideae* with two genera, *Polyporoideae* with 17 genera, and the *Hymenochaetoideae* with three genera. These genera were based partly on anatomical, partly on morphological characters as interpreted by Pilát, partly on the basis of Patouillardian, partly on the basis of Donkian concepts.

Imazeki, working in Japan (1943), published a monographic treatment of species in Japan and the nearby islands and Asiatic mainland. In his treatment he placed 38 genera in four tribes and seven subtribes. These categories include: *Polyporeae* with the subtribes *Trametinae* with six genera, *Coriolinae* with five genera, *Tyromycetinae* with five genera, *Piptoporinae* with three genera, *Fometinae* with two genera, *Favolinae* with two genera, and *Polyporinae* with three genera; *Ganodermeae* with three genera; *Mucronoporeae* with eight genera; and the *Cryptoporeae* with one genus. In 1953 Imazeki established the family *Phylacteriaceae* in which he included Donk's tribe *Boletopseae*. This family includes related thelephoraceous, hydnaceous, cantharellaceous, and polyporaceous genera.

Pinto-Lopes presented a study of the biosystematics of the *Polyporaceae* in 1952. While the system proposed by Cunningham is based on a modification of the Corner hyphal system concepts, Pinto-Lopes found the system of little value and proposed a system based

on the type of thickening of the hyphae forming the fruit body as they matured and aged, coupled with the presence or absence and type of clamp connections. This system has been vigorously criticized by Corner (1954) although the concept of tertiary or modified hyphae has considerable value in any system based on the study of hyphal systems as the only, principal or even secondary basis for polypore systematics. Pinto-Lopes set up seven subfamilies in which he included 22 genera. An attempt was made to prepare a system applicable to the polypores of the world. The *Cladodendroideae*, of uncertain position, include one genus; the *Leptoporoideae* include six genera; the *Trametoideae* include four genera; the *Phaeochroideae* include four genera; the *Cladomeroideae*, of uncertain position, include one genus, the *Mensulari-oideae* include two genera, and the *Xanthochroideae* include four genera. Most genera used by Pinto-Lopes have been emended from the original description by him or by earlier workers. The system ignores characters other than the hyphae and leaves much to be desired in its application to the *Polyporaceae*.

Overholts (1953) left a manuscript at his death in November 1946 which has been prepared for publication by J. L. Lowe. "The Polyporaceae of the United States, Alaska and Canada" follows the conventional Overholts pattern of generic usage. *Merulius* and *Poria* are not treated in the book but are keyed out in the main key to genera. The book includes eight genera, not segregated into subfamilies, tribes or subgenera. The genera with the number of species treated for North America north of Mexico are as follows: *Fomes*, 40 species; *Lenzites*, five species; *Cyclomyces*, one species; *Daedalea*, seven species; *Hexagona*, one species; *Trametes*, 13 species; *Favolus*, six species; *Polyporus*, 162 species. Each species is well illustrated. The generic concepts are in some cases fuzzy to say the least. For instance, *Trametes* species are keyed out with *Polyporus* although treated separately. In the generic key the following statement is made: "No one realizes better than I how difficult, even impossible, it is to recognize a species of *Trametes* on the basis of this character." In the discussion of the genus the following remark is found: "One eventually, after much experience, acquires a more or less practical concept of its typical characters." Thus to Overholts *Trametes* was a necessary but confused concept in the family to be recognized only by intuition.

In 1941 Bondartsev and Singer, in their System of the Polyporaceae, found that a number of new names was needed for categories in their concepts of generic limits. These names were used in the key to the genera which they published. These names were genuine *nomina nuda* unless one wishes to assign key characters the rank of generic diagnoses in which case they are only partial *nomina nuda* since no Latin diagnoses were published in 1941. Supposedly the Latin diagnoses were to be supplied in a paper by Bondartsev to be published almost simultaneously in a Russian journal. Since this paper, if published, was not available in the United States in 1944, Singer published a short paper in Mycologia validating the genera which needed such action. One of the genera (*Merulioporia*) was considered not to need validation since it was an orthographic variant of a genus validly published in the meantime by Murrill (*Meruliporia*).

Shortly after copies of Bondartsev's book (1953) on Russian polypores became available the writer was able to borrow a copy from John A. Stevenson. Through the kindness of Dr. Benjamin S. Levine a translation of pertinent parts of this book, and of two earlier papers, was prepared. Bondartsev and Singer (1943) published a paper on the natural system of the pore fungi. In this no genera were validated but an outline of their system was presented together with arguments for the various categories described. All genera were distributed among five families in the *Aphyllophorales*, one of two orders in the *Gymnocarpi*, one of three subclasses in the *Basidiomycetes*. Each family happens to occur in a different one of the five suborders of this order. The *Corticiineae* include two families which contain polyporaceaus genera: The *Corticiaceae* have several polypores assigned to them while the *Meruliaceae* include only genera with porose hymenophores. The *Fistulinaceae* are assigned to the *Cyphelliineae*, the *Boletopsidaceae* to the *Phylacteriineae*, the *Scutigeraceae* to the *Clavariineae* and the *Polyporaceae* to the *Polyporiineae*. Except in discussion the subfamilial categories are not introduced here.

Bondartsev and Singer (1950) published a guide to the collection of higher basidial fungi for scientific study. In this paper, which is primarily for the well informed layman and student, a key is presented to the major groups of the Basidiomycetes. It is of interest to note that while the key to the Agaricales approximates the 1949 system of Singer, the key to the polypores is a Russian translation of Killermann's key published in 1928. Thus the 1941, 1943, and the forthcoming 1953 treatments are completely ignored.

The largest volume on polypores to have been published to date was that of Bondartsev (1953). This book includes 725 pages and 187 plates in which are described and illustrated 270 species in 61 genera of polypores. Many of the species are divided into varieties and forms. The *Polyporaceae, sensu stricto* are divided into a number of subfamilies and tribes as follows: *Poroideae* with eight resupinate genera; *Tyromycetoideae* with seven genera; *Fomitoideae: Piptoporeae* two genera, *Ischnodermateae* three genera, *Fomiteae* two genera, *Phaeoleae* 1 genus, *Inonoteae* seven genera and *Ganodermateae* one genus; *Polyporoideae* with two genera; *Corioloideae: Corioleae* 12 genera, *Oxyporeae* four genera, *Hirschioporeae* one genus and *Daedaleae* four genera. The major key to genera is essentially that published by Bondartsev and Singer in 1941 except that additional information and discussion have been inserted and Latin diagnoses for all new Bondartsev and Singer genera are included following the appearance of a new generic epithet in the key. This did not validate these genera since Singer (1944) had already done that. Again *Merulioporia* is dropped in favor of *Meruliporia* Murr.

Kotlaba and Pouzar (1957–58), in Prague, espoused the hyphal system technique of studying polypores and based their system of European polypore genera on Bondartsev's work extended to include narrower generic limits made necessary by more strict generic definitions. On the results of their own studies, and on those of others, they accepted 48 genera, seven of which were novelties. Since they considered only species occurring in Czechoslovakia, the system they

suggest remains less complete than that of Bondartsev. No key to these genera was presented either in the Czech language nor in the lengthy English summary. It is unfortunate that these workers were not more critical in their apparently hurried adoption and systematization of this technique of studying polypores.

This summary discloses that no two groups of arrangements are similar. Some treatments show resemblances to others. When used in the Friesian sense, the family *Polyporaceae* is divided differently from treatment to treatment. When used in the sense of Patouillard, the Aphyllophoraceae or Aphyllophorales, possibly better called Polyporales are likewise treated differently by each group of workers.

Lazaro (1915–16), Torrend (1924), and Lloyd (Stevenson and Cash, 1936) produced sets of interesting genera. Lazaro worked in Spain without, apparently, benefit of much literature on the subject of the polypores. He produced a number of interesting genera, most of which are invalid. Torrend, in a discussion of Brazilian polypores, raised all of the sections of *Polyporus* and *Polystictus* used by Lloyd to generic rank. There is nothing of particular value to Torrend's work, most, if not all, the names being invalid for one reason or another as indicated below. Lloyd, under the pseudonym of McGinty, created six generic names applicable to polypore genera if they can be proven necessary. The following quotation from a recent paper by Donk (1950) should be of considerable interest to students of fungi who must deal with names by the late lamented Prof. N. J. McGinty.

"*General remarks on the McGinty names.*—C. G. Lloyd coined and published several names in a jocular spirit. Thus, in his Mycological Writings, a facetious Prof. McGinty acted as the author of a number of new names, of which, in the present paper, *Aleurocystus* is a good example. Lloyd's intention was to ridicule and imitate certain mycologists he labeled as 'name jugglers', 'splitters', and 'new species hunters'. One point emerges incontestibly: the McGinty names were not acceptable to Lloyd himself, the publishing author. However, he repeatedly admonished future authors not to forget the existence of the McGinty names, which he apparently considered validly published. This is clear: these names belong to the class of nomina provisoria! Not being accepted by the publishing author they were 'merely proposed in anticipation of the future acceptance of the group concerned, or of a particular circumscription, position, or rank of the group', and hence were not validly published. Many of the McGinty names were often purposely and somewhat maliciously coined after bad examples, and served as punishment in store for those who dared to deviate from the usually rather crude taxonomical views to which Lloyd adhered. A number of the names in question were published as nomina nuda. Some were taken up by subsequent authors and validly published on such an occasion.

"Stevenson and Cash, in their valuable 'The new fungus names proposed by C. G. Lloyd' (in Bull. Lloyd Libr. No. 35, 1936) brought together all of that author's new names, inclusive of McGinty's. Several of these names were originally accompanied by insufficient descriptions or were perfect examples of nomina nuda. To such names the two compilers added Lloyd's own herbarium notes when available and when

not previously published; these notes often amount to descriptions. They were offered purely as a matter of record and Stevenson and Cash (p. 2) were careful in pointing that out in their book: 'No attempt has been made to evaluate or to discuss critically the species (and genera) here listed. For instance, we have included most of the names published by Lloyd under the "nom-de-plume" N. J. McGinty as a matter of record since upon critical study a few of them at least may be found (taxonomically) valid'. Therefore, in their compilation one will find McGinty names effectively republished and some of them with an accompanying description, but it is evident that in the light of Art. 37 bis, the 'publishing authors', in this case Stevenson and Cash, did not ensure their valid publication. They had no intention to do so ('incidental mention')"

In the following list of genera the usage of each genus published after the time of Murrill's treatment of the Polyporaceae in North American Flora, and the usage of each monographer after Murrill, will be indicated with each generic category, valid or invalid, together with the type, in Friesian terms, and the writer's reasons for believing the genus invalid if it is considered invalid. Synonymy will also be indicated where it appears to be of interest.

THE LIST OF GENERA

ABORTIPORUS Murr., Torr. Bot. Cl. Bull. **31:** 422. 1904.

Type: *Daedalea biennis* Fr.

Bondartsev and Singer considered this identical with *Heteroporus* Laz. and made it a synonym of that genus; however, that genus, being of later date, and based on the same species, is an obligate synonym of this. Accepted by Kotlaba and Pouzar in its original sense. See also O. Fidalgo's characterization of this genus.

AGARICON Adans., Fam. Pl. **2:** 10. 1763.

Type: Not based on a binomial.

Invalid: Pre-Friesian.

AGARICUS (Dill.) L., Sp. Pl. **1176**. 1753.

Type: *A. quercinus* L. in the sense of Murrill, which is *Daedalea quercina* Pers. ex Fr. Used by Murrill for species of *Daedalea* between 1905 and 1906 after which it was discarded. Not *Agaricus* Fr., 1821.

Invalid: Pre-Friesian.

AGARICUS (Dill. ex L.) Murr., Torr. Bot. Cl. Bull. **32:** 83. 1905.

Type: *Daedalea quercina* Pers. ex Fr.

Invalid: A later homonym of *Agaricus* L. ex Fr., 1821, Agaricaceae.

ALBATRELLUS Mich. ex S. F. Gray, Nat. Arr. Brit. Pl. **1:** 645. 1821.

Type: *Polyporus albidus* Pers. (probably *P. ovinus* Schaeff. ex Fr.).

The second species placed here by S. F. Gray is considered a variety of *Polyporus brumalis* by Pilát. Accepted by Kotlaba and Pouzar for essentially the same group of polypores.

AMAURODERMA Murr., Torr. Bot. Cl. Bull. **32:** 366. 1905.

Type: *Fomes regulicolor* M. C. Cooke.

Keyed out by Pilát in the *Ganodermoideae* but not discussed because species do not occur in the region treated by him; used by Imazeki in the tribe *Ganodermeae*.

AMPHITRETIA Hill., Hist. Pl. **2.** 1751.

Type: None cited.

Invalid: Pre-Friesian.

AMYLOCYSTIS Bond. & Sing. in Singer, Mycologia **36:** 67. 1944.

Type: *Polyporus lapponicus* Romell.

Protonym: *Amylocystis* Bond. & Sing., Ann. Mycol. **39:** 53. 1941, *nomen nudum*.

The genus was established to include polypores with amyloid cystidia and was used by its authors in the *Tyromycetoideae* of the *Polyporaceae*. Kotlaba and Pouzar use this genus.

AMYLOPORIA Bond. & Sing. in Singer, Mycologia **36:** 67. 1944.

Type: *A. calcea* (Fr.).

Protonym: *Amyloporia* Bond. & Sing., Ann. Mycol. **39:** 50. 1941, *nomen nudum*.

A segregate of the large and complex genus *Poria*, placed by its authors in the *Poroideae* of the *Polyporaceae*.

ANISOMYCES Pilát, in Kavina and Pilát, Atlas. **3:** 331. 1940.

Type: *Polyporus odoratus* Wulf. ex Fr.

Invalid: *Nomen nudum* (published without Latin diagnosis; a later homonym of *Anisomyces* von Hoehnel, Ascomycetes). It was erected for dark colored context species of *Trametes*. It is a synonym of *Gloeophyllum* Karst. Rather than meaning "a fungus without symmetry", the name refers to the "anise"-like odor of the fresh specimens of the type species.

ANTRODIA Karst., Faun. Fl. Fenn. Medd. **5:** 40. 1879.

Type: *Daedalea mollis* Sommerf. ex Fr.

This genus possibly is not distinct from *Trametes* Fr., and is placed by Bondartsev and Singer in the *Corioleae* of the *Corioloideae* in the *Polyporaceae*. Used by Imazeki in the *Coriolinae* of the *Polyporeae*. Accepted by Kotlaba and Pouzar for use in the "*Trametes*-complex".

APORPIUM Bond. & Sing. in Singer, Mycologia **36:** 67. 1944.

Type: *A. canescens* (Karst.).

Protonym: *Aporpium* Bond. & Sing., Ann. Mycol. **39:** 50. 1941, *nomen nudum*.

A segregate from the genus *Poria* placed by its authors in the *Poroideae* of the *Polyporaceae*. Teixeira and Rogers (1955) have shown that the basidia are cruciate septate so that, in spite of the fact that the species has true pores, this genus is assigned to the Tremellaceae.

APUS Nees v. Esenbeck ex S. F. Gray, Nat. Arr. Brit. Pl. **1:** 617. 1821.

Type: Based on material now referred to *Schizophyllum* and *Lenzites*—see Donk 1949: 377. The first species is *A. albeus* Nees, a

synonym of *Schizophyllum commune* Fr. Considered synonymous with *Schizophyllum* by Singer in Lilloa **22:** 259. 1949.

ASCHERSONIA Endl., Add. **103**. 1842.
non *Aschersonia* Mont., 1856.
Type: *Laschia crustacea* Jungh.
Erected to replace *Laschia* Jungh. and *Junghuhnia* Corda; replaced by *Bizzozeriella* and *Underwoodina* O. Kuntze, the latter of which may be the correct one.
Included with the polypores because of the porose hymenium.

ASTEROCHAETE (Pat.) Bond. & Sing., Ann. Mycol. **39:** 58. 1941.
Type: *A. megalopora* (Mont.) Bond. & Sing.
Separated from *Polyporus* s. str. on the basis of the presence of setae, which are roughened, and placed by Bondartsev and Singer with *Polyporus* in the *Polyporoideae* of the *Polyporaceae*.

ASTEROSTROMELLA Hoehn. & Litsch., Ak. Wien **116:** 773. 1907.
Type: *A. epiphylla* Hoehn. & Litsch.
This genus is considered synonymous with *Vararia* Karst. by Rogers and Jackson (1943); used by Singer for two species segregated from *Poria* which, on the basis of Rogers and Jackson's interpretation, are transferrable to *Vararia*.

AURANTIOPORELLUS Murr., Torr. Bot. Cl. Bull. **32:** 486. 1905.
Type: *Polyporus alboluteus* Ell. & Ev.
Pilát and Pinto-Lopes considered this a synonym of *Phaeolus*. Used by Kotlaba and Pouzar in their generic listings.

AURANTIOPORUS Murr., Torr. Bot. Cl. Bull. **32:** 487. 1905.
Type: *Polyporus croceus* Pers. ex Fr.
Pinto-Lopes placed this in *Hapalopilus*. Accepted by Kotlaba and Pouzar for use in their system.

BAEOSTRATOPORUS Bond. & Sing. in Singer, Mycologia **36:** 68. 1944.
Type: *B. braunii* (Rab.).
Protonym: *Baeostratoporus* Bond. & Sing., Ann. Mycol. **39:** 62. 1941, *nomen nudum*.
This genus was placed by the authors in the *Oxyporeae* of the *Corioloideae* in the *Polyporaceae*.

BIZZOZERIELLA O. Kuntze, Rev. Gen. **3**(2): 538. 1898.
Type: *B. basicystis* O. Kuntze.
See *Aschersonia* Endl.

BJERKANDERA Karst., Soc. Faun. Fl. Fenn. Medd. **5:** 38. 1879.
Type: *Polyporus adustus* Willd. ex Fr.
Used by Donk in the *Tyromyceteae* of the *Polyporoideae*; included by Bondartsev and Singer in the *Tyromycetoideae* of the *Polyporaceae*; placed by Imazeki in the *Tyromycetinae* of the *Polyporeae*; used by Pinto-Lopes in the *Leptoporoideae* with the addition of *Merisma* Gill. to the concept of the type; accepted for use by Kotlaba and Pouzar.

BOLETOPSIS Fayod, Malph. **3:** 72. 1889.
Type: *Boletus leucomelas* Pers. (spelled *Polyporus melaleucas* by

Fayod according to Singer) which is *Polyporus subsquamosus* γ *leucomelas* Mich. ex Fr.

This genus is the basis and only genus of Donk's tribe *Boletopseae* of the subfamily *Phylacterioideae*; placed by Bondartsev and Singer in the *Boletopsidaceae* of the *Phylacteriineae*; placed by Imazeki in the *Boletopseae* of the *Phylacteriaceae*; Kotlaba and Pouzar use this genus as a member of Imazeki's family *Phylacteriaceae*.

BOLETUS Dill. ex S. F. Gray, Nat. Arr. Brit. Pl. **1:** 640. 1821.

Type: *Polyporus caesius* Schrad. ex Fr.

Invalid: A later homonym of *Boletus* Dill. ex Fr., 1821, Boletaceae. The type species is usually included in the genus *Tyromyces* Karst. so that Gray's genus becomes a synonym of that genus.

BONDARZEWIA Singer, Rev. de Mycol. **5:** 4. 1940.

Type: *Polyporus montanus* Quél.

Used by Bondartsev and Singer in the *Scutigeraceae* of the *Clavariineae*; by Imazeki in the *Polyporinae* of the *Polyporeae*. To accommodate this genus, together with at least one clavariaceous and one hydnaceous segregate, Kotlaba and Pouzar erected the family *Bondarzewiaceae*.

BOUDIERA Lazaro, R. Acad. Cienc. Madr. Rev., **14:** 835. 1915–16.

Type: *B. connata* (Batr.).

Invalid: A later homonym of *Boudiera* Cooke, 1877, an Ascomycete. Possibly a synonym of *Coltricia* S. F. Gray.

BRESADOLIA Speg., Fung. Guar. **1:** 15. 1883.

Type: *B. paradoxa* Speg.

Invalid: Teratologic. Lloyd apparently considered this a good genus.

BUGLOSSUS Wahl., Fl. Upsal. 459. 1820.

Type: *B. quercinum* Wahl.

Invalid: Pre-Friesian. A synonym of *Fistulina* Huds. ex Fr.

BULLIARDIA Lazaro, R. Acad. Cienc. Madr. Rev. **14:** 839. 1915–16.

Type: *Polyporus unicolor* Bull. ex Fr.

Invalid: A later homonym of *Bullardia* Jungh. 1830, and of *Bulliarda* Necker 1790, which are considered orthographic variants. The type of this genus is considered to be the type of *Cerrena* Mich. ex S. F. Gray, so that *Bulliardia* Lazaro would be an obligate synonym of that genus.

BYSSOCORTICIUM Bond. & Sing. in Singer, Mycologia **36:** 69. 1944.

Type: *B. atrovirens* (Fr.).

Protonym: *Byssocorticium* Bond. & Sing.

Used by Bondartsev and Singer in the *Corticiaceae* of the *Corticiineae* and including segregates of *Poria*.

CALOPORIA Karst., Finl. Basidsv. Suppl. **2:** 23. 1893.

Type: *Polyporus violaceus* Fr.

This genus is another segregate of *Poria*.

CALOPORUS Karst., Rev. Myc. **3**(9): 18. 1881.
Type: *Polyporus incarnatus* Pers. ex Fr.
Invalid: *Nomen nudum*. Replaced later by *Caloporia* Karst.

CALOPORUS Quél., Ench. Fung. 164. 1886.
Type: *Polyporus subsquamosus* L. ex Fr.
Invalid: A later homonym of *Caloporus* Karst., 1881, *nomen nudum*, Polyporaceae. Used by Pilát for species assigned to *Albatrellus*, *Scutiger*, *Boletopsis*, etc., by other workers. An obligate synonym of *Albatrellus*.

CARTILOSOMA Kotlaba and Pouzar, Česká Mykologie **12**: 101, 103. 1958.
Type: *Trametes subsinuosa* Bres.
A segregate for a monomitic, subresupinate, trametoid polypore.

CELLULARIA Bull., Herb. France, p. 9, pl. 414. 1788.
Type: *Agaricus betulinus* L.
Invalid: Pre-Friesian. A synonym of *Lenzites* Fr.

CELLULARIA Bull. ex O. Kuntze, Rev. Gen **3**(2): 451. 1891.
Type: *Daedalea betulina* L. ex Fr.
Invalid: An obligate synonym of *Lenzites* Fr.

CERAPORIA Donk, Rev. **2**: 170. 1933.
Type: *Poria viridans* (Berk. & Br.) Sacc.
A segregate of *Poria* based on *Poria* sect. *Chrooporae* Bourd. & Galz. and placed in the *Tyromyceteae* of the *Polyporoideae*; Bondartsev and Singer spell this *Ceraporus* and place it in the *Poroideae* of the *Polyporaceae*.

CERATOPHORA Humb., Fl. Friberg 112. 1793.
Type: *C. fribergensis* Humb., an abnormal form of *Polyporus odoratus* Wulf. ex Fr.
Invalid: Pre-Friesian, teratologic. A synonym of *Gloeophyllum*.
Used by Bondartsev and Singer as a normal genus and placed in the *Ischnodermateae* of the *Fomitoideae* in the *Polyporaceae*.

CERIOMYCES Corda, in Sturm, Deutsch.-Krypt. Fl. **3**: 133, t. 61. 1837.
Type: *C. fischeri* Corda.
Invalid: Teratologic.

CERIOPORUS Quél., Ench. Fung. 167. 1886.
Type: *Polyporus squamosus* Huds. ex Fr.
Invalid: An obligate synonym of *Polyporus* Fr., sensu Murrill. However, valid but a synonym of *Polyporus* Fr. in the sense of Donk.

CERRENA Mich. ex S. F. Gray, Nat. Arr. Brit. Pl. **1**: 649. 1821.
Type: *Polyporus unicolor* Bull. ex Fr.
A segregate of *Daedalea* Fr. Used by Murrill, and accepted for use by Kotlaba and Pouzar.

CERRENELLA Murrill, Torr. Bot. Cl. Bull. **32**: 361. 1905.
Type: *Irpex tabacinus* Berk. & Curt.
A segregate of *Irpex* Fr.

CHAETOPORELLUS Bond. & Sing. in Singer, Mycologia **36:** 67. 1944.
Type: *C. latitans* (Bourd. & Galz.).
Protonym: *Chaetoporellus* Bond. & Sing., Ann. Mycol. **39:** 50. 1941, *nomen nudum.*
A segregate of *Poria*, included by its authors in the *Poroideae* of the *Polyporaceae.*

CHAETOPORUS Karst., Hedw. **28:** 148. 1890.
Type: *C. tenuis* Karst.
A segregate of *Poria* included by Bondartsev and Singer in the *Poroideae* of the *Polyporaceae.*

CHORIPHYLLUM Velenovsky. (Cited in a list of genera but no reference found.)
Type: ?
Invalid: *Nomen nudum.* Not recognized by Pilát in his monograph.

CLADODENDRON Lazaro, R. Acad. Cienc. Madr. Rev. **14:** 863. 1915–16.
Type: *Polyporus frondosus* Schrank. ex Fr.
Invalid: An obligate synonym of *Grifola* S. F. Gray.
Used by Pinto-Lopes for the type species, and species assignable otherwise to *Polyporus*, *Grifola*, and *Boletopsis*, as the only genus of his *Cladodendroideae.*

CLADOMERIS Quél., Ench. Fung. 167. 1886.
Type: *Polyporus umbellatus* Pers. ex Fr.
Pinto-Lopes used this genus in the *Cladomerioideae* for species otherwise included in *Laetiporus* and *Grifola.* Based on the type, this is a synonym of *Grifola* although not obligate.

CLADOSPORUS Chev., Fung. 1837.
Type: *C. fulvus* Chev.
Invalid: Teratologic.

CLIMACOCYSTIS Kotlaba and Pouzar, Česká Mykologie **12:** 95, 103. 1958.
Type: *Polyporus borealis* Fr.
Proposed for a species of central stemmed polypores whose cystidia resemble those of certain hydnaceous fungi in that they have metachromatic granules which stain in cresyl blue.

COLTRICIA Mich. ex S. F. Gray, Nat. Arr. Brit. Pl. **1:** 644. 1821.
Type: *Polyporus perennis* L. ex Fr.
Used by Cunningham in the *Fomiteae* for stipitate brown-context species including *Phaeolus* and certain substipitate and imbricate species; by Imazeki for stipitate brown context species in the *Mucronoporeae*; and most recently by Coker who discussed species of the eastern United States. Many people have preferred to use *Polystictus* Fr. for this group, although strictly speaking *Coltricia* antendates this genus and is the correct name. For a discussion of the suggested conservation of *Polystictus* over *Coltricia* see Rogers, 1950. Applied by Kotlaba and Pouzar to coltricioid fungi in the *Phellinaceae* of Imazeki.

COLTRICIELLA Murr., Torr. Bot. Cl. Bull. **31:** 348. 1901.
Type: *P. dependens* Berk. & Curt.
Coker (1947) considered this a synonym of *Coltricia* (in spite of the different spores) and transferred the type and only species to that genus.

CORIOLELLUS Murr., Torr. Bot. Cl. Bull. **32:** 481. 1905.
Type: *Trametes sepium* Berk.
This genus is a segregate of *Trametes* Fr. It is included by Bondartsev and Singer in the *Corioleae* of the *Corioloideae* in the *Polyporaceae*. Accepted for use by Kotlaba and Pouzar.

CORIOLOPSIS Murr., Torr. Bot. Cl. Bull. **32:** 358. 1905.
Type: *Polyporus occidentalis* Klotzsch.
This is another trametoid segregate and was used by Bondartsev and Singer in the *Corioleae* of the *Corioloideae* in the *Polyporaceae*.

CORIOLUS Quél., Ench. Fung. 175. 1886.
Type: *Polyporus versicolor* L. ex Fr.
Donk used this genus in the *Daedaleae* of the *Polyporoideae* and included *Cerrena* and *Poronidulus* as synonyms; Bondartsev and Singer included this in the *Corioleae* of the *Corioloideae* in the *Polyporaceae*; Cunningham included *Pycnoporus* as a synonym in this genus with the species of the original concept; and Imazeki used this in the *Corioliineae* of the *Polyporeae*. Pilát placed this complex in the genus *Trametes* as did Kotlaba and Pouzar.

CRISTELLA Pat., Hym. D'Eur. 151. 1887.
Type: *C. cristata* (Pers. ex Fr.) Pat.
Invalid: A synonym of *Sebacina* (Tremellales). Rogers (Mycologia **36:** 78, 1944), states: "This is certainly the preferable name for the genus under discussion [*Trechispora* Karst. sensu Bond. & Sing.] . . . ." "Since, however, the only possible generic type is *Thelephora cristata* (Pers.) Fr., which presumably is a *Sebacina*, *Cristella* must fall into synonymy with that genus. At least, that seems to be the meaning of the type concept here." He concluded his discussion with the statement that since *T. cristata* is probably the same as *Sebacina incrustans*, *Cristella*=*Sebacina*. On the other hand, Donk (Fungus **27:** 19, 1957) states that he ". . . pointed out that the name *Cristella* has to be applied in agreement with the fungus on which it was based rather than with the type of the specific name wrongly applied to its only species . . . ." On this basis he uses *Cristella* rather than *Phlebiella* or *Trechispora* for species like *Poria candidissima*.

The writer has been caught in this trap twice. On the first occasion, at the suggestion of D. P. Rogers, he applied Donk's usage of *Cristella* in making the combination *Cristella candidissima* (Schw.) Donk in W. B. Cooke, Mycologia **35:** 288. 1943. Following the publication of Rogers' conclusions concerning the correct name for application to *Trechispora*, the transfer was made to *Phlebiella* resulting in the combination *P. candidissima* (Schw.) W. B. Cooke, Mycologia **44:** 253. 1952. This combination is also attributed to Singer who suggested in discussion that the sense in which Bondartsev and Singer used *Trechispora* should in reality be applied to *Phlebiella*. Thus the combination *Trechispora candidissima* (Schw.) Bond. & Sing. in Sing., Mycologia is

available for those who prefer to use *Trechispora* in the sense of Bond. & Sing. for resupinate fungi not assignable to the genus *Sistotrema* or its resupinate segregate *Trechispora* sensu Rogers.

The principle adopted by the Amsterdam Congress, quoted by Rogers, indicates that Rogers' treatment is correct, and Article 55 of the 1956 edition of the International Code does not appear to disagree with this. Thus the genus *Phlebiella* is considered here to be the valid taxon for this concept.

CRYPTODERMA Imazeki, Bull. Tokyo Sci. Mus. **6:** 106. 1943.
Type: *Polyporus ribis* Schum. ex Fr.
Invalid: Synonymy includes the monotypic genus *Porodaedalea* Murr. with which this genus should become synonymous. Erected by Imazeki for species of *Phellinus* with a trichoderm on the pileus surface. The name is illegitimate under Art. 64, par. 1.

CRYPTOPORUS (Pk.) Hubbard, Canad. Ent. **24:** 250. 1892.
Type: *Polyporus volvatus* Pk.
Bondartsev and Singer included this with *Piptoporus* in the *Piptoporeae* of the *Fomitoideae* in the *Polyporaceae*; Imazeki established the *Cryptoporeae* on this the only genus he assigned to the tribe.

CRYPTOPORUS (Pk.) Shear, Torr. Bot. Cl. Bull. **29:** 450. 1902.
Type: *Polyporus volvatus* Pk.
Invalid: A later homonym and synonym of *Cryptoporus* (Pk.) Hubbard, 1892.

CUBAMYCES Murr., Torr. Bot. Cl. Bull. **32:** 480. 1905.
Type: *Polyporus cubensis* Mont.
Reduced by Murrill to synonymy under *Trametes* in N. Am. Fl. **9:** 43. 1907.

CYANOSPORUS Lloyd, as McGinty, Myc. Writ. **3:** 436. Aug. 1909.
Type: *Polyporus caesius* Schrad. ex Fr.
The type is usually included in the genus *Tyromyces* Karst. On page 75 of their treatment of Lloyd names, Stevenson and Cash say: "Based on *Polyporus caesius* (Schrader) Fr. and 'characterized by the blue spores in mass'. Lloyd did not take this proposed new genus seriously, since he did not recognize it in naming specimens of *P. caesius* in his herbarium. Lloyd's name is mentioned by Saccardo (Syll. Fungorum **21:** 282. 1922) but apparently not accepted."

CYCLOMYCES Fr., Linnaea **5:** 512. 1830.
Type: *C. fuscus* Fr.
Placed by Bondartsev and Singer in the *Inonoteae* of the *Fomitoideae* in the *Polyporaceae*; used by Imazeki in the *Mucronoporeae*; used by Overholts for *C. greenei*. See *Cycloporus* Murr.

CYCLOMYCETELLA Murr., Torr. Bot. Cl. Bull. **31:** 422. 1904.
Type: *Boletus pavonius* Hook.
Not considered distinct from *Coriolus* Quél. by most authors.

CYCLOPORELLUS Murr., Torr. Bot. Cl. Bull. **34:** 468. 1907.
Type: *Polyporus iodinus* Mont.
Not considered distinct from *Cyclomyces* Fr. by most authors.

CYCLOPORUS Murr., Torr. Bot. Cl. Bull. **31:** 423. 1904.

Type: *Cyclomyces greenei* Berk.

Placed by Bondartsev and Singer in the *Inonoteae* of the *Fomitoideae* in the *Polyporaceae*; found to be an extreme variant of a species of *Coltricia* by Gilbertson and Lowe.

DAEDALEA Fr., Syst. Myc. **1:** 332. 1821.

Lectotype: *D. biennis* Bull. ex Fr. according to Patouillard, Ess. Taxon. 95. 1900.

Invalid: A homonym of *Daedalea* Fr.—see below.

The type species is assigned to *Abortiporus* Murr. and *Heteroporus* Laz. Singer (Lloydia **8:** 141. 1945) removed the rough spored *Abortiporus subabortivus* Murr. to his new genus *Diacanthoides* as a synonym of the type species *D. phillippinensis* (Pat.) Singer. Murrill (Mycologia **43:** 376. 1951) indicates that Stevenson thinks the Patouillardian species of doubtful value; apparently good material was not available for examination of spores. See also Fidalgó's recent discussion of *Abortiporus*.

Lectotype: *Daedalea quercina* L. ex Fr.

This species, from the dimidiate section of *Daedalea*, is chosen as the type of the genus rather than *D. biennis* of the stipitate section because the genus has been used universally in the sense typified by *D. quercina* from the time of Persoon, Fries and S. F. Gray to the present. See the discussion by Singer in Lilloa **22:** 731. 1949; and by O. Fidalgo in Taxon **7:** 133. 1958. Bondartsev and Singer used this genus in the *Daedaleae* of the *Corioloideae* in the *Polyporaceae*; used by Donk in the strict sense of the type species in the *Daedaleae* of the *Polyporoideae*; Cunningham uses the genus, as typified by this species, but in the sense of species with brown context including *Gloeophyllum*, although he combines *D. unicolor* in *Lenzites* rather than in *Trametes*; Imazeki uses this in the *Trametinae* of the *Polyporeae*; Pilát makes this a synonym of *Trametes* which is a later genus; used by Overholts in the most inclusive sense; used by Kotlaba and Pouzar in a broad sense.

DAEDALEOPSIS Schroet., Krypt. Fl. Schles. **3:** 492. 1889.

Type: *Daedalea confragosa* Pers. ex Fr.

This genus is a segregate from *Daedalea* including species with thin dissepiments. Used by Donk in the *Daedaleae* of the *Polyporoideae*; by Bondartsev and Singer in the *Daedaleae* of the *Corioloideae* in the *Polyporaceae*; by Imazeki in the *Trametinae* of the *Polyporeae*; Pilát includes this as a synonym of *Trametes*.

DAEDALEOIDES Lazaro, R. Acad. Cienc. Madr. Rev. **14:** 675. 1915–16.

Type: *D. pinicola* Lazaro.

The type of this genus, and thus the genus, is probably assignable to a member of the existing *Daedalea* complex, genera all dating before 1900.

DAEDALEA Raf., Anal. Tab. Tshb. Univ. 211. 1815.

Type: None listed.

Invalid: Pre-Friesian. Probably an orthographic variant of *Daedalea*. Merrill, 1949, indicates that this is the same as *Daedalea* Pers.

DENDROPHAGUS Murr., Torr. Bot. Cl. Bull. **32:** 473. 1905.
Type: *Polyporus colossus* Fr.
Invalid: A later homonym of *Dendrophagus* Toumey, 1900. Schizomycetes.

DIACANTHODES (Pat.) Singer, Lloydia **8:** 141. 1945.
Type: *D. philippinensis* (Pat.) Singer.
See discussion by Murrill who did not see the spores.

DICTYOPANUS Pat., Ess. Taxon. 137. 1900.
Type: *Polyporus rhipidium* Berk.
Treated by Singer in "The *Laschia* Complex" as a member of the *Pleurotoideae* of the *Tricholomataceae* in the *Agaricales*. Listed with the polypores because of the porose hymenium and its otherwise usual inclusion in *Favolus*.

EARLIELLA Murr., Torr. Bot. Cl. Bull. **32:** 478. 1905.
Type: *E. cubensis* Murr.
Distinguishable from other species of *Trametes* by its laccate crust.

ECHINODONTIUM Ell. & Ev., Torr. Bot. Cl. Bull. **27:** 49. 1900.
Type: *E. tinctorium* Ell. & Ev.
Typonym: *Echinodontium* Ellis in Lloyd, Myc. Writ. **1:** 3. 1898. Incidental mention.
Usually classed with the *Hydnaceae*, but apparently more closely allied with mucronoporaceous polypores.

ELFVINGIA Karst., Krit. Ofvers. Finl. Basidsv. 333. 1889.
Type: *E. lipsiensis* (Batsch.) which is *Polyporus applanatus* Pers. ex S. F. Gray.
This type is a synonym of *Ganoderma applanatum* and thus this genus becomes a synonym of *Ganoderma* Karst. unless the genus is segregated; Imazeki used this at first as a subgenus of *Ganoderma*, then as a segregate of *Ganoderma* in the *Ganodermeae*. Used by Kotlaba and Pouzar as a genus in the *Ganodermataceae* Donk: *Elfvingia* has a dimitic trama, *Ganoderma* is trimitic.

ELFVINGIELLA Murr., Northern Polypores 52, 1914.
Type: *Polyporus fomentarious* L. ex Fr.
Invalid: An obligate synonym of *Fomes* Kickx.

ELMERIA Bres., Hedw. **51:** 317. 1911.
Lectotype: *Hexagona vespacea* Pers.
A pileate segregate of *Hexagona* in which two species are listed. The second species is chosen as the type because it is the better known of the two based on the cited references and synonyms.

ELMERINA Bres., Ann. Mycol. **10:** 507. 1912.
Type: *Poria setulosa* P. Henn.
A segregate of *Poria* with daedaleoid pores. Neither species cited with *Elmeria* is mentioned except by implication. This name was erected because the spelling of *Elmeria* appeared to be too close to *Elmera* Rydberg 1905, Saxifragaceae. When Rydberg published *Elmera* there was no indication of the basis for the name since the

species, on which the name was based was collected by Suksdorf on Mount Adams, Washington, and Rydberg did not cite a reason for choosing the name. *Elmeria* and *Elmerina* were named for the collector of Philippine fungi, A. D. E. Elmer. *Elmeria* Bresadola is not considered an orthographic variant of *Elmera* Rydberg. Since the species assigned to the "genus" in each of the publications are not necessarily related, one being a segregate of *Hexagona*, the other of *Poria*, the two genera are considered valid and usable subject to demonstration of their synonymy or lack of synonymy with other genera.

ENSLINIA Fr., Sum. Veg. Scand. **2:** 399. 1849.
Type: *E. pocula* Fr.
Invalid: A later homonym of *Enslinia* Reichenb., 1828.

FAVOLASCHIA Pat. in Morat, Journ. Bot. 1887: 231. 1887.
Type: *F. auriscalpium* Mont.
Included here because of the porose hymenium.

FAVOLASCHIA (Pat.) Henn., Engler's Bot. Jahrb. **22:** 93. 1895.
Type: *F. gaillardii* Pat.
See Singer, in Lloydia **8:** 170–230. 1945; and Lilloa **22:** 732. 1949. Included here because of the porose hymenium.

FAVOLUS Fr., Elench. Fung. 22. 1828.
Type: *F. brasiliensis* Fr.
Used by most workers including Overholts; considered a synonym of *Polyporus* Fr. *sensu stricto* by Singer and by Pilát.

FAVOLUS Pal. de Beauv., Fl. Owar. **1:** 1, pl. 1. 1805.
Type: *F. hirtus* Pal. de Beauv.
Invalid: Pre-Friesian. See Donk's (1933) discussion of the confusion in types and concepts between pre-Friesian concepts of *Favolus* and *Hexagona*, and Fries' treatment of these genera.

FIBULOPORIA Bond. & Sing. in Singer, Mycologia **36:** 67. 1944.
Type: *Polyporus molluscus* Pers. ex Fr.
Protonym: *Fibuloporia* Bond. & Sing., Ann. Mycol. **39:** 49. 1941, *nomen nudum*.
A segregate of *Poria* placed by the authors in the *Poroideae* of the *Polyporaceae*.

FISTULINA Bull. ex Fr., Syst. Myc. **1:** 396. 1821.
Type: *F. hepatica* Huds. ex Fr.
Listed here because of the apparent porose nature of the hymenophore. Included by Donk in the *Fistulinoideae*; by Pilát in the *Fistulineae*; and by Bondartsev and Singer in the *Fistulinaceae* of the *Cyphelliineae*.

FLABELLOPILUS Kotlaba and Pouzar, Česká Mykologie **11:** 155. 1957.
Type: *Polyporus giganteus* Pers. ex Fr.
Erected for monomitic, flabelliform polypores without clamp connections.

FLAVIPORELLUS Murr., Torr. Bot. Cl. Bull. **32:** 425. 1905.
Type: *Polyporus splitgerberi* Mont.
Possibly a tropical segregate of *Laetiporus* Murr.

FLAVIPORUS Murr., Torr. Bot. Cl. Bull. **32:** 360. 1905.
Type: *Polyporus rufoflavens* Berk. & Curt.

FOMES Kickx, Flore Crypt. des Flandres **2:** 237. 1867.
Lectotype: *Fomes fomentarius* L. ex Fr.

Three groups of species are included in Kickx's list of perennial polypores in the cited reference. In addition to the species representing *Fomes* in the restricted sense, there was a species assignable to *Ganoderma* in the broad sense, and two assignable to *Phellinus*. Cunningham has chosen *Fomes salicinus* (Fr.) Kickx as the type of the genus *Fomes* Kickx, thus including only the brown context perennial species in the genus. This was done on the basis of the doctrine of residues, the other three species having been previously assigned to other genera. Thus in Cunningham's sense, *Fomes* Kickx becomes a synonym of *Phellinus* Quél. So far no one has tried to replace *Ganoderma* with this genus. Hilborn and Linder, in calling attention to this genus, emphasized *Fomes igniarius* without specifically considering it as the lectotype of *Fomes* Kickx, and in 1941 the writer chose this species as the type of the genus. Patouillard, in 1900, indicated by the names of the tribe and subgenus to which he assigned *Fomes ignarius* that he considered this species the type of *Phellinus* Quél. Donk attributed this genus to Gillet, as many workers still do, but cited the type as here listed. He placed it in the *Daedaleae* of the *Polyporoideae*, and included *Fomitopsis* as a synonym. Bondartsev and Singer limited this genus to the lectotype on the basis of large spores and of tramal color, and included it with *Fomitopsis* in the *Fomiteae* of the *Fomitoideae* in the *Polyporaceae*; Pilát used the genus in the sense of Donk; Cunningham used it in his *Fomiteae*; Imazeki used it in the *Fometinae* of the *Polyporeae*; and Kotlaba and Pouzar accepted it only in the sense of the type. Used by Overholts and by Lowe in the most extensive sense. Teixeira's discussion (1958) of this species is of interest.

FOMITELLA Murr., Torr. Bot. Cl. Bull. **32:** 365. 1905.
Type: *Polyporus supinus* Sw. ex Fr.

A segregate of *Fomes* or *Polyporus* based on the olive colored context.

FOMITIPORELLA Murr., N. Am. Fl. **9:** 12. 1907.
Type: *Poria umbrinella* Bres.

A segregate of the brown Porias probably synonymous with *Physisporus* Chev.

FORMITIPORA Murr., N. Am. Fl. **9:** 7. 1907.
Type: *F. langloisii* Murr.

Lowe (Lloydia **11:** 167. 1948) indicates that this species is a synonym of *Poria punctata* (Fr.) Karst., the resupinate form of *Fomes robustus* Karst. Thus the genus would become untenable and a synonym of *Phellinus* Quél. In 1958, Lowe (Lloydia **21:** 109) places this species in synonymy with *Poria umbrinella* Bres. in which case the genus *Fomitiporia* would become an obligate synonym of *Fomitiporella*.

FOMITOPSIS Karst., Soc. Faun. Fl. Fenn. Medd. **6:** 9. 1881.
Type: *Polyporus pinicolus* Sw. ex Fr.

Not considered distinct from *Fomes* Kickx by many workers.

Bondartsev and Singer include this with *Fomes* in the *Fomiteae* of the *Fomitoideae* in the *Polyporaceae*; Imazeki placed this in the *Fometinae* of the *Polyporeae*; Cunningham used this, for species otherwise assigned to *Fomes* Kickx, in the Polyporeae; used by Pinto-Lopes, in about the sense of the type as indicated above, in the *Trametoideae*; Kotlaba and Pauzar accept this genus in a rather restricted sense.

FRIESIA Lazaro, R. Acad. Cienc. Madr. Rev. **14:** 587. 1915–16.

Type: *F. applanata* (Pers.) Gill.

Invalid: An obligate synonym of *Elfvingia* Karst., and thus a synonym of *Ganoderma* Karst. for those who do not separate these two genera.

FULVIFOMES Murr., Northern Polypores 49. 1914.

Type: *Pyropolyporus robiniae* Murr.

A segregate of *Pyropolyporus* Murr. based on colored spores. If species of *Phellinus* (of which *Pyropolyporus* is an obligate synonym) with colored spores can be segregated, this will be the available genus; the type would be *Fomes rimosus*, of which this species is a synonym in the sense of North American workers only, although Lowe (1958) now recognizes *Fomes robiniae* (Murr.) Lowe as a species distinct from *F. rimosus* (Berk.) Cke.

FUNALIA Pat., Ess. Taxon. 95. 1900.

Type: *Polyporus mons-veneris* Mont.

Bondartsev and Singer use this in the *Corioleae* of the *Corioloideae* in the *Polyporaceae*; accepted by Kotlaba and Pouzar for two European species.

FUSCOPORELLA Murr., N. Am. Fl. **9:** 6. 1907.

Type: *F. corruscans* Murr.

A segregate of the brown context Porias. Lowe (Lloydia **11:** 166. 1948) indicated that *F. corruscans* is the same as *Fomitiporella floridana* Murr. so that the genus becomes a synonym of *Fomitiporella*. In 1958 Lowe (Lloydia **21:** 109) placed the type in synonymy with *Poria umbrinella* Bres. thus making *Fuscoporella* an obligate synonym of *Fomitiporella*. Possibly not distinct from *Physisporus* Chev.

FUSCOPORIA Murr., N. Am. Fl. **9:** 3. 1907.

Type: *Polyporus ferruginosus* Schrad. ex Fr.

A segregate of the brown context Porias. Not considered distinct from *Physisporus* Chev. In the sense of Donk (1941: 174) this would become an obligate synonym of *Poria* (Pers.) em Karst. In the sense of Cunningham this includes all resupinate brown context species of *Poria*; he placed it in the *Poriae*.

GANODERMA Karst., Rev. Myc. **3**(9)**:** 17. 1881.

Type: *Polyporus lucidus* Leyss. ex Fr.

Donk placed this in the *Ganodermoideae* as did Pilát, both included *Elfvingia* as a synonym; Imazeki used this in the *Ganodermeae* but segregated *Elfvingia* as a separate genus; Bondartsev and Singer used this genus but deemphasized the importance of the spores placing it in the *Ganodermateae* of the *Fomitoideae* in the *Polyporaceae*; Pinto-Lopes placed this in the *Phaeochroideae* and added *Fomes* ss. str., and *Elfvingia;*

accepted by Kotlaba and Pouzar for trimitic members of the *Ganodermataceae*.

GLOBIFOMES Murr., Torr. Bot. Cl. Bull. **31:** 424. 1904.
Type: *Polyporus graveolens* Schw. ex Fr.

GLOEOPHYLLUM Karst., Hattsv. **2:** x, 79. 1879.
non *Gloeophyllum* O. A. Korshikov (Chlorophyta), 1953.
Type: *Daedalea sepiaria* Wulf. ex Fr.
Used by Donk and included in the *Daedaleae* of the *Polyporoideae*; Pilát uses this as does Donk; placed by Bondartsev and Singer in the *Daedaleae* of the *Corioloideae* in the *Polyporaceae*; used by Imazeki in the *Trametinae* of the *Polyporeae*; used in the sense of the type by Pinto-Lopes who added *Anisomyces* of Pilát and placed it in the *Phaeochroideae*; accepted by Kotlaba and Pouzar for some of the species usually assigned to this genus.

GLOEOPORUS Mont., Ann. Sci. Nat., Bot. II. **17:** 126. 1842.
Type: *G. conchoides* Mont.
Considered merulioid by Murrill and so not treated with the polypores in North American Flora. Used by Donk in the *Tyromyceteae* of the *Polyporoideae*; Pilát gave this genus a double value adding *Bjerkandera* as a second subgenus; Bondartsev and Singer used this in the *Tyromycetoideae* of the *Polyporaceae*; used by Imazeki in the *Tyromycetinae* of the *Polyporeae*; used by Pinto-Lopes in the original sense with an additional species from *Coriolus*; accepted by Kotlaba and Pouzar in the sense of the type. These writers include *P. amorphus* at first but later removed this species to the new genus *Skeletocutis*.

GRIFOLA Mich. ex S. F. Gray, Nat. Arr. Brit. Pl. **1:** 643. 1821.
Type: *Polyporus frondosus* Schrank. ex Fr.
Used by Pilát for species assignable to this genus as well as for *Laetiporus* and *Bondarzewia*; used by Imazeki in the *Polyporinae* of the *Polyporeae*; accepted by Kotlaba and Pouzar in the sense of the type.

GYROPHANA Pat., Cat. rais. Pl. Tunisie 53. 1897.
Type: *Merulius lacrimans* Schum. ex Fr.
Invalid: An obligate synonym of *Serpula* Pers. ex S. F. Gray. Used by Bondartsev and Singer for species of the *Serpula* type in the *Meruliaceae* of the *Corticiineae*.

GYROPHORA Pat., Hym. Eur. 143. 1887.
Type: *Merulius lacrimans* Schum. ex Fr.
Invalid: A later homonym of *Gyrophora* Ach., 1803, Lichenes, and an obligate synonym of *Serpula* Pers. ex S. F. Gray.

HANSENIA Karst., Soc. Faun. Fl. Fenn. Medd. **5:** 40. 1879.
Type: *Polyporus hirsutus* Schrad. ex Fr.
Invalid: A later homonym of *Hansenia* Turcz.; a synonym of *Coriolus* Quél.

HAPALOPILUS Karst., Rev. Myc. **3**(9)**:** 18. 1881.
Type: *Polyporus nidulans* Fr.
Used by Donk who included *Phaeolus* and *Pycnoporellus* as synonyms and included it in the *Tyromycetineae* of the *Polyporoideae*; Bondartsev

and Singer used this in the *Tyromycetoideae* of the *Polyporaceae*; Imazeki placed it in the *Tyromycetinae* of the *Polyporeae*; Pinto-Lopes used this in the *Leptoporoideae* adding *Aurantioporus* to the genus; accepted by Kotlaba and Pouzar for the type only.

HAPLOPORUS Bond. & Sing. in Singer, Mycologia **36:** 68. 1944.
Type: *Polyporus odorus* Sommerf. ex Fr.
Protonym: *Haploporus* Bond. & Sing., Ann. Mycol. **39:** 60. 1941, *nomen nudum*.
A segregate of *Trametes* Fr., used by its authors in the *Corioleae* of the *Corioloideae* in the *Polyporaceae*.

HEMIDISCIA Lazaro, R. Acad. Cienc. Madr. Rev. **14:** 575. 1915–16.
Type: *Polyporus lacteus* Fr.
Invalid: An obligate synonym of *Irpex* Fr.

HENNINGSIA Möll., Protobasid. 44. 1895.
Type: *H. geminella* Möll.

HETEROBASIDION Bref., Unters **8:** 154. 1889.
Type: *Polyporus annosus* Fr.
Not considered distinct from *Fomes* Kickx sensu lato. Used by Pinto-Lopes for the type species in the *Mensularioideae*; accepted by Kotlaba and Pouzar but only in the sense of the type.

HETEROPORUS Lazaro, R. Acad. Cienc. Madr. Rev. **15:** 119. 1915–16.
Type: *Daedalea biennis* Bull. ex Fr.
Invalid: An obligate synonym of *Abortiporus* Murr. Donk emended this, simplifying the description, and included it in the *Daedaleae* of the *Polyporoideae*; Pilát used it in the sense of Donk; Bondartsev and Singer use this in the *Oxyporeae* of the *Corioloideae* of the *Polyporaceae*; Pinto-Lopes uses the genus in the sense of the type species in the *Leptosporoideae*; see also the discussion by O. Fidalgo in Taxon **7:** 133. 1958.

HEXAGONA Poll., Pl. Nov. 35, pl. 2–3, 1816.
Type: *H. alveolaris* DC.
Invalid: Pre-Friesian. Fries converted this concept to *Favolus*.

HEXAGONA Fr., Epicrisis 496. 1838.
Type: *H. apiaris* Fr.
Also spelled *Hexagonia*. Used by Bondartsev and Singer in the *Corioleae* of the *Corioloideae* in the *Polyporaceae*; Imazeki placed this in the *Trametinae* of the *Polyporeae*; Pinto-Lopes placed this in the *Phaeochroideae;* used by Overholts and others in the Friesian sense; Kotlaba and Pouzar typify the genus with *Favolus tenuiculus* Palis. They recognize one European species, *H. nitida* Mont., but indicate that it may be a *Daedalea*.

HIRSCHIOPORUS Donk, Rev. **2:** 162. 1933.
Type: *Polyporus abietinus* Dicks. ex Fr.
Erected by Donk for this and related species on the basis of the cystidia and the hymenophoral configuration; Bondartsev and Singer separated this into the *Hirschioporeae* of the *Corioloideae* in the *Poly-*

poraceae; Imazeki used it in the *Corioleae* of the *Polyporeae*; accepted by Kotlaba and Pouzar who would exclude "*Trametes pergamena*".

HOLOGLOEA Pat., Ess. Taxon. 85, 1900.
Type: *H. microspora* Pat.
Included here because of the porose nature of the hymenophore.

HYDNOCHAETE Pk., N. Y. St. Mus. Rept. **50:** 113. 1897.
Type: *H. setigera* Pk.
Invalid: A later homonym of *Hydnochaete* Bres., 1896, *Thelephoraceae*. Replaced by *Hydnochaetella* Sacc. Used by Imazeki in the *Mucronoporeae*.

HYDNOCHAETELLA Sacc., Tab. Com. gen. fung. **14:** 11. 1898.
Type: *Hydnochaete setigera* Pk.

HYDNOFOMES P. Henn., Bot. Jahrb. **28:** 269. 1900.
Type: *H. tsugicola* P. Henn.
A later synonym of *Echinodontium* Ell. & Ev.

HYDNOPHYSA Clements, Gen. Fung. 108. 1909.
Type: A re-spelling of *Hydnofomes* erected by Clements to prevent mixtures in orthography.
Invalid: *Nomen nudum*. An obligate synonym of *Hydnofomes*, a synonym of *Echinodontium*.

HYDNOPORIA Murr., N. Am. Fl. **9:** 3. 1907.
Type: *Hydnum squalidum* Fr. (Synonyms: *Sistotrema fuscescens* Schw., *Irpex cinnamomeus* Fr.).
According to one interpretation, this is a synonym of *Hydnochaete* Pk. thus a synonym of *Hydnochaetella* Sacc.

HYMENOGRAMME Mont. & Berk., Lond. Journ. Bot. **3:** 329. 1844.
Type: *H. javensis* Mont. & Berk.

HYMENOGRAMME Berk. & Mont., in Mont., Syll. Crypt. 151. 1856.
Type: *H. javensis* Berk. & Mont.
Invalid: An obligate synonym of *Hymenogramme* Mont. & Berk.

HYPODRYS Pers., Myc. Eur. **2:** 148. 1825.
Type: *Fistulina hepatica* Huds. ex Fr.
Invalid: An obligate synonym of *Fistulina* Huds. ex Fr.

INODERMA Karst., Soc. Faun. Fl. Fenn. Medd. **5:** 39. 1879.
Type: *Polyporus radiatus* Sow. ex Fr.
Invalid: A later homonym of *Inoderma* S. F. Gray, 1821, Lichenes.

INODERMUS Quél., Ench. Fung. 173. 1886.
Type: *Polyporus cuticularis* Bull. ex Fr.
Invalid: An obligate synonym of *Inonotus* Karst.

INONOTUS Karst., Soc. Faun. Fl. Fenn. Medd. **5:** 39. 1880.
Type: *Polyporus cuticularis* Bull. ex Fr.
Donk included this in the *Hymenochaetoideae* where it was also placed by Pilát who considered resupinate as well as pileate species in it; Bondartsev and Singer used this in the *Inonoteae* of the *Fomitoideae*

of the *Polyporaceae*; Imazeki placed this in the *Mucronoporeae*; Cunningham included it in his *Fomiteae* for non-perennial, non-resupinate, non-stipitate species with brown context; accepted in the sense of Pilát's emendation by Kotlaba and Pouzar for use in the *Hymenochaetaceae*.

IRPICIPORUS Murr., Torr. Bot. Cl. Bull. **32:** 451. 1905.
Type: *Irpex mollis* Berk. & Curt.
No considered superficially distinct from *Irpex* Fr. Accepted in the sense of the type by Kotlaba and Pouzar.

IRPICIOCHAETE Rick, Ann. Mycol. **38:** 58. 1940.
Type: *I. nodulosus* Rick.
Possibly not distinct from *Hydnochaetella* Sacc.

IRPEX Fr., Elench. Fung. 142. 1828.
Lectotype: *Irpex lacteus* Fr. according to Cunningham 1949: 2.
Cunningham considered *I. pendulum* Fr. as a member of the *Hydnaceae* and used *Irpex* for strongly irpiciform polypores; Donk placed *Irpiciporus* in synonymy and included this in the *Daedaleae* of the *Polyporoideae*; Bondartsev and Singer included this in the *Oxyporeae* of the *Corioloideae* in the *Polyporaceae*; Kotlaba and Pouzar accepted this genus in the emended sense of Donk using *Hydnum pendulum* (A. & S.) Fr. as type and including both *I. pendulum* and *I. lacteus*. For a discussion of the typification of this genus see Donk (Taxon **5:** 100–101, 1956).

ISCHNODERMA Karst., Soc. Faun. Fl. Fenn. Medd. **5:** 38. 1880.
Type: *Polyporus resinosus* Schrad. ex Fr.
Used by Donk who placed it in the *Daedaleae* of the *Polyporoideae*; Pilát used it in the same sense; Bondartsev and Singer placed it in the *Ischnodermateae* of the *Fomitoideae* in the *Polyporaceae*; used by Imazeki in the *Piptoporinae* of the *Polyporeae*; used by Pinto-Lopes in the *Leptoporoideae*; accepted by Kotlaba and Pouzar in the sense of Murrill.

JUNGHUHNIA Corda, Anal. Mycol. 195. 1842.
Type: *J. crustacea* (Jungh.).
Invalid: A later homonym of *Junghuhnia*. Cf. *Aschersonia*.

KORDERA Adans., Fam. Pl. **2:** 10. 1763.
Type: None listed.
Invalid: Pre-Friesian. According to O. Kuntze this is *Sesia* Adans. which is a synonym of *Merulius* Hall. ex Fr.

LACCOCEPHALUM McAlp. & Tepp., R. Soc. Victoria Proc., n. s. **7:** 166. 1895.
Type: *L. basilopiloides* McAlp. & Tepp.

LAETIPORUS Murr., Torr. Bot. Cl. Bull. **31:** 607. 1904.
Type: *Polyporus sulphureus* Bull. ex Fr.
Used by Imazeki in the *Tyromycetinae* of the *Polyporeae*; Bondartsev and Singer used this in the *Tyromycetoideae* of the *Polyporaceae*; accepted for use by Kotlaba and Pouzar.

LARICIFOMES Kotlaba and Pouzar, Česká Mykologie **11:** 158. 1957.
Type: *Polyporus officinalis* Vill. ex Fr.
Established for a single species for a discussion of which see Teixeira (Mycologia **50:** 671. 1958).

LASCHIA Junghuhn, Batav. Gen. Kunt. wet. verh. **17:** 74. 1838–9.
Type: *L. crustacea* Junghuhn.
Invalid: A later homonym of *Laschia* Fr., 1830. Cf. *Aschersonia* Endl. Placed in this list because of the poroid hymenium. See Singer, 1945, 1949.

LENZITES Fr., Gen. Hymen. 10. 1836.
Type: *L. betulina* (L. ex Fr.) Fr.
Used by Donk in the *Daedaleae* of the *Polyporoideae*; by Imazeki in the *Trametinae* of the *Polyporeae*; by Bondartsev and Singer in the *Daedaleae* of the *Corioloideae* in the *Polyporaceae*; by Pilát as a synonym of *Trametes*; by Cunningham as a probable member of the *Polyporeae*; used by Overholts in the most inclusive sense; accepted by Kotlaba and Pouzar for use in their system. See O. Fidalgo, 1958, for additional nomenclatural discussion.

LENZITINA Karst., Final. Basidsv. 337. 1889.
Type: *Daedalea sepiaria* Wulf. ex Fr.
Invalid: An obligate synonym of *Gloeophyllum* Karst.

LEPTOPORA Raf., Journ. de Bot. (Desv.) **2:** 177. 1809.
Type: *L. nivea* Raf.
Invalid: Pre-Friesian.

LEPTOPORUS Quél., Ench. Fung. 175. 1886.
Type: *L. epileucus* (Fr.).
Murrill considered this genus synonymous with *Bjerkandera* Karst.; Pilát used this genus for *Tyromyces* adding as synonyms *Spongipellis* and *Caloporia*; used by Pinto-Lopes for species assigned by others to *Tyromyces*.

LEUCOFOMES Kotlaba and Pouzar, Česká Mykologie **11:** 157. 1957.
Type: *Polyporus ulmarius* Sow. ex Fr.
Apparently Kotlaba and Pouzar erected this genus in the sense of Pinto-Lopes use of *Mensularia* Lazaro although the Lazaro genus was erected for a phellinoid species. Since Lowe (1958) indicated that *P. ulmarius* has been considered a member of *Rigidoporus* Murr., it is possible that this genus is superfluous.

LEUCOPHELLINUS Bond. & Sing. in Singer, Mycologia **36:** 68. 1944.
Type: *L. irpicioides* (Bond. ap. Pilát).
Protonym: *Leucophellinus* Bond. & Sing.
Used by the authors in the *Inonoteae* of the *Fomitoideae* in the *Polyporaceae*.

LEUCOPORUS Quél., Ench. Fung. 165. 1886.
Type: *L. lepideus* (Fr.).
Not considered distinct from *Polyporus* Fr., ss. str.

LIGNOSUS Torrend, Broteria, Ser. Bot. **20:** 107. 1922.
Type: Based on the *Lignosus* section of Lloyd's Stipitate Polypores.
See introductory notes on Torrend genera.

LINDTNERIA Pilát, Studia botanica Cechica **1:** 72. 1938.
Type: *L. trachyspora* (Bourd. & Galz.) Pilát.
A segregate of *Poria* based on rough spores, this type being one of the species included in the genus *Trechispora* by Bondartsev and Singer. See *Cristella*.

LOXOPHYLLUM Klotzsch in mss. as synonym of *Cyclomyces* Kunze in Hooker, Bot. Miscell. **2:** 150. 1831.
Type: *L. velutinum* Kunze, in mss.
Invalid: *Nomen nudum*.

MELANOPORELLA Murr., N. Am. Fl. **9:** 14. 1907.
Type: *Polyporus carbonaceus* Berk. & Curt.
A segregate of the dark context species of *Poria* not considered distinct from *Melanoporia* Murr.

MELANOPORIA Murr., N. Am. Fl. **9:** 14. 1907.
Type: *Polyporus niger* Berk.
A segregate of the dark context species of *Poria*.

MELANOPUS Pat., Hym. Eur. 137. 1887.
Type: *Polyporus squamosus* Huds. ex Fr.
Not considered distinct from *Polyporus* Fr. ss. str.

MENSULARIA Lazaro, R. Acad. Cienc. Madr. Rev. **14:** 736. 1915–16.
Type: *Polyporus radiatus* Sow. ex Fr.
Not considered distinct from *Inonotus* Karst.; used by Pinto-Lopes in the *Mensularioideae* for a species usually assigned to *Fomitopsis* in the sense used above.

MERIPILUS Karst., Bidr. Finl. Nat. Folk **37:** 33. 1882.
Lectotype: *Polyporus giganteus* Pers. ex Fr.
Not considered distinct from *Grifola* S. F. Gray.

MERISMA Gill., Champ. **1:** 688. 1878.
Type: *M. imberbis* (Fr.) Gill.
Invalid: A later homonym of *Merisma* Schw., 1822, and *Merisma* S. F. Gray, 1821.

MERISMA Torrend, Broteria, Ser. Bot. **21:** 35. 1923.
Type: Based on Lloyd's section *Merismus* of *Polyporus* and *Polystictus*.
Invalid: Later homonym of *Merisma* S. F. Gray, 1821, *Merisma* Schw., 1822, and *Merisma* Gill., 1878. See notes above on Torrend genera.

MERULIOPORIA Bond. & Sing., Ann. Mycol. **39:** 48. 1941.
Type: *M. taxicola* (Pers.).
Invalid: *Nomen nudum*. Erected for certain *Merulius*-like species of *Poria*, placed in the *Meruliaceae* of the *Corticiineae* by its authors.

This genus was not validated by Singer or by Bondartsev with the other Bondartsev and Singer generic novelties because Murrill's *Meruliporia* was published validly before validation could be effected. Since Murrill's *Meruliporia* is based on an entirely different organism another name will have to be suggested for the merulioid Porias if it is thought that they are generically distinct.

MERULIPORIA Murr., Mycologia **34:** 596. 1942.
Type: *M. incrassata* (Berk. & Curt.).
A segregate of *Poria* for a species morphologically unlike but physiologically like *Serpula*.

MERULIUS Haller, Hist. Stirp. 1768.
Type: *Cantharellus cibarius* Fr. according to Earle, 1909.
Invalid: Pre-Friesian.

MERULIUS Hall. ex Fr., Syst. Myc. **1:** 326. 1821.
Type: *Merulius tremellosus* Schrad. ex Fr.
Considered a genus of the *Meruliaceae*. Burt, Cunningham, and most workers include the genus *Serpula* in *Merulius*. Bondartsev and Singer separated these genera but included both in the *Meruliaceae* of the *Corticiineae*. In his notes Overholts used this genus in its broadest sense.

MERULIUS S. F. Gray, Nat. Arr. Brit. Pl. **1:** 636. 1821.
Type: *Cantharellus aurantiacus* Schaeff. ex Fr.
Invalid: A later homonym of *Merulius* Hall. ex Fr., 1821, *Meruliaceae*. The type is referred by many to the genus *Clitocybe* in the *Agaricaceae*, although Singer (1949) placed it in *Hygrophoropsis* in the *Paxillaceae* of the *Agaricales*.

MERULIUS Hall ex O. Kuntze, Rev. Gen. Pl. **2:** 861. 1891.
Type: *M. albidus* Fr.
Invalid: A later homonym of *Merulius* Hall. ex Fr., 1821, *Meruliaceae*.

MICROPORELLUS Murr., Torr. Bot. Cl. Bull. **32:** 483. 1905.
Type: *Polyporus dealbatus* Berk. & Curt.
Not considered distinct from *Polyporus* Fr., ss. str.

MICROPORUS Pal. de Beauv., Fl. Owar. **1:** 12. 1805.
Type: *M. perula* Pal. de Beauv. (*Polyporus xanthopus* Fr.).
Invalid: Pre-Friesian.

MICROPORUS Beauv. ex O. Kuntze, Rev. Gen. Pl. **3**(2)**:** 494. 1898.
Type: *Polyporus concinnus* Beauv. ex Fr.
Not considered distinct from *Coltricia* S. F. Gray. Used by Imazeki in the sense of *Polyporus* Fr., ss. str., in the *Favolinae* of the *Polyporeae*.

MISON (Grae.) Adans., Fam. Pl. **2:** 10. 1763.
Type: Not based on a binomial.
Invalid: Pre-Friesian.

MUCILAGO Hoffm., Bot. Taschenb., pl. 12, f. 2. 1795.
Type: *M. reticulata* Hoffm.
Invalid: Pre-Friesian. A later homonym of *Mucilago* Mich. ex Adans., 1763, Myxomycetes. A synonym of *Merulius* Hall. ex Fr., 1821.

MUCRONOPORUS Ell. & Ev., Journ. Mycol. **5:** 28. 1889.
Type: *Polyporus balansae* Speg.
Not considered distinct from *Inonotus* Karst. on the basis of the type, but including species of several genera which are characterized by the presence of setae in the hymenium, whether perennial or not. Imazeki (1954) has suggested that poroid members of the *Hymenochaetaceae* be placed in a family based on this genus, the *Mucronoporaceae*.

MYRIADOPORUS Pk., Bull. Torr. Bot. Cl. **11:** 27. 1884.
Type: An abnormal form of *Polyporus adustus* Willd. ex Fr.
Invalid: Teratologic.

NIGROFOMES Murr., Torr. Bot. Cl. Bull. **32:** 425. 1904.
Type: *Polyporus melanoporus* Mont.
Possibly assignable to *Phellinus*; Cunningham reported seeing setae; Lowe could not find them.

NIGROPORUS Murr., Torr. Bot. Cl. Bull. **32:** 361. 1905.
Type: *Polyporus vinosus* Berk.

OCHROPORUS Schroet., Krypt. Fl. Schles. **3:** 483. 1889.
Type: *Polyporus contiguus* Pers. ex Fr. which is a synonym of *Polyporus igniarius* L. ex Fr.
Invalid: An obligate synonym of *Phellinus* Quél. Donk used this genus instead of *Phellinus*, placing it in the *Hymenochaetoideae*, and including *Porodedalea* as a synonym.

OLIGOPORUS Bref., Unters. **8:** 114. 1889.
Type: *O. farinaceus* Bref.
Not considered distinct from *Tyromyces* Karst.

ONNIA Karst., Finl. Basidsv. 326. 1889.
Type: *Polyporus tomentosus* Fr.
Considered by some a synonym of *Coltricia* S. F. Gray; used by Imazeki in the *Mucronoporeae*.

OSMOPORUS Singer, Mycologia **36:** 67. 1944.
Type: *Polyporus odoratus* Wulf. ex Fr.
An obligate synonym of *Anisomyces* Pilát which is a *nomen nudum* and thus could be replaced by this if the group is considered distinct from *Gloeophyllum* and *Trametes*.

OVINUS Torrend, Broteria, Ser. Bot. **22:** 13. 1924.
Type: Based on section *Ovinus* of Lloyd's Stipitate Polypores.
This heterogenous assemblage includes species assigned to *Albatrellus*, *Polyporus*, etc.; see notes above on Torrend genera.

OXYPORUS Donk, Rev. **2:** 202. 1933.
Type: *Polyporus populinus* Schum. ex Fr.
Erected by Donk for *Coriolus* sect IV *Oxporus* Bourd. & Galz. and placed in the *Daedaleae* of the *Polyporoideae*; used by Pilát in the sense of Donk; used by Cooke (1949) in the sense of Donk; Bondartsev and Singer placed this in the *Oxyporeae* of the *Corioloideae* in the *Poly-*

poraceae; used by Imazeki in the *Corioleae* of the *Polyporeae*; accepted by Kotlaba and Pouzar in the sense of Donk.

OXYURIS Lloyd, as McGinty, Myc. Writ. **4:** Fomes 261, f. 600. Jan. 1915.

Type: *Fomes pachyphloeus* Pat.

A second way of spelling this name is *Oxyuria*.

Invalid: A later homonym of *Oxyuris* Linstrow, 1907. Stevenson and Cash, 1936: 95, say concerning this genus: "Lloyd, more or less facetiously, suggests this name for polypores with the peculiar imbedded cystidia or setae characteristic of *Fomes pachyphloeus* Pat., which species would become the type. Later (Myc. Writ. **4:** L. 54, 7 Jan. 1915) he suggests that *Poria weirii* belongs to the genus, citing it, however, as *Oxyuria* rather than *Oxyuris*. The name may be ignored since Lloyd did not use it except for the above brief mention. Furthermore the name has been preempted by *Oxyuris* Linstrow, Centr. Bakt. **44:** 265. 1907.

PELLOPORUS Quél., Ench. Fung. 166. 1886.

Type: *Polyporus triqueter* Fr.

Considered a synonym of *Inonotus* and *Onnia*. Bondartsev and Singer interpreted *P. triqueter* in the sense of Quélét as *P. corrugis* Fr. and placed this genus in the *Ischnodermateae* of the *Fomitoideae* in the *Polyporaceae*; Kotlaba and Pouzar followed this interpretation.

PELLOPORUS Torrend, Broteria, Ser. Bot. **22:** 6. 1924.

Type: Based on section *Perennes* of Lloyd's Stipitate Polypores.

Invalid: A later homonym of *Pelloporus* Quél., 1886, *Polyporaceae*. See notes above on Torrend genera.

PERENNIPORIA Murr., Mycologia **34:** 595. 1942.

Type: *Polyporus unitus* Pers. ex Fr.

Since the type is one of the Porias usually called *P. medulla-panis*, in the sense of Donk, 1949: 105, this would be invalid since it is an obligate synonym of *Poria* Pers. ex S. F. Gray em. M. C. Cooke.

PETALOIDES Torrend, Broteria, Ser. Bot. **21:** 17. 1923.

Type: Section *Petaloides* of Lloyd's Stipitate Polypores

See comment on other polypore genera of Torrend.

PHAEOCORIOLELLUS Kotlaba and Pouzar, Česká Mykologie **11:** 162. 1957.

Type: *Daedalea trabea* Pers. ex Fr.

This genus was established for a species usually assigned to the genus *Gloeophyllum*. The English summary of the paper in which this genus was published gives no clear reason for this separation or for ignoring other genera which could have been used.

PHAEODAEDALEA Lloyd, as McGinty, Myc. Writ. **4:** L. 44: 9. Jan. 1913.

Type: *Daedalea sprucei* Lloyd.

Stevenson and Cash, 1936: 95, say concerning this genus: "This is another of the taxonomic pleasantries of the late Prof. N. J. McGinty and is 'Based on globose, colored spores'. The genus (sic) is referred

to on several occasions (Myc. Writ. **4:** L. 44: 9, Jan. 1913; **4:** L. 60: 15, Dec. 1915; 5: L. 65: 14, March 1917), *Daedalea sprucei* being the type assigned. Except for the above fleeting references, the name was not used by Lloyd in formal publication, in labeling specimens in his collection, or elsewhere as far as known".

PHAEOLOPSIS Murr., Torr. Bot. Cl. Bull. **32:** 489. 1905.
Type: *Polyporus verae-crucis* Berk.

PHAEOLUS Pat., Ess. Taxon. 86. 1900.
Type: *Polyporus schweinitzii* Fr.

In the earlier treatment by this writer (1941) this genus was referred to *Hapalopilus*. Cunningham has recently transferred the type species to *Coltricia*. Bondartsev and Singer separated this into the *Phaeolaea* in the *Fomitoideae* of the *Polyporaceae*; Pilát placed *Hapalopilus*, *Pycnoporellus*, *Aurantioporus* and *Aurantioporellus* in synonymy with this genus; Imazeki used this in the *Mucronoporeae*; Pinto-Lopes used this in the *Xanthochroideae* for the type species with which he placed *Aurantioporellus*; accepted by Kotlaba and Pouzar in the sense of Bondartsev and Singer and placed in the *Hymenochaetaceae*.

PHAEOPORUS Schroet., Krypt. Fl. Schles. **3:** 489. 1889.
Type: *Polyporus obliquus* Pers. ex Fr.

Considered by Donk a synonym of *Inonotus*, but if *Physisporus* Chev. is recognized this must be considered an obligate synonym in the resupinate series; or it is a synonym of *Phellinus* in the pileate sense.

PHAEOTRAMETES Lloyd, as McGinty, Myc. Writ. **4:** 355–6. June 1915.
Type: *Hexagona decipiens* Berk.

Stevenson and Cash, 1936: 95, have the following to say about this genus: "Lloyd transfers *Hexagona decipiens* Berk. to *Polyporus* remarking in passing that, 'Properly it is a "new genus" *Phaeotrametes* McGinty, on the same principle (colored spores) that other similar new genera, *Phaeoradulum*, *Phaeocyphella*, etc., were manufactured'. Later he states that the species which he described as new as *Polyporus deceptivus* 'by rights goes in McGinty's genus *Phaeotrametes*'. The name was not used in labeling specimens."

PHELLINUS Quél., Ench. Fung. 172. 1886.
Lectotype: *Polyporus igniarius* L. ex Fr.

Patouillard selected the type when he designated the section and subgenus in which the genus and species were placed from the specific name of the type. Used by Pilát who included as synonyms the following genera: *Ochroporus*, *Pyropolyporus*, *Porodaedalea*, *Fuscoporia* and *Hapalopilus*; Bondartsev and Singer placed this in the *Inonotae* of the *Fomitoideae* in the *Polyporaceae*; Imazeki used this in the *Mucronoporeae*; Pinto-Lopes used this in the *Xanthochroideae* in the sense of the type with such additional groups as *Porodaedalea*, *Cryptoderma* and certain species of *Hapalopilus*; accepted by Kotlaba and Pouzar for use in the *Hymenochaetaceae*.

PHLEBIELLA Karst., Hedw. **29:** 271. 1890.
Type: *Phlebia vaga* Fr.

A corticioid genus with poroid as well as corticioid species which includes segregates from *Poria*. Karsten's *Trechispora* is partly

synonymous at least in the sense of Bondartsev and Singer, and of Singer. Through a printer's error this has been spelled *Phlebriella* Karst. See also *Cristella* Pat.

PHORIMA Raf., Med. Repos. II. **3:** 423. 1806.

Type: *P. betulina* Raf. which is *Favolus* Beauv. 1805, fide Desv., Jour. Bot. **4:** 275. 1814, non *Favolus* Fr., 1821, according to Murrill, 1949.

Invalid: Pre-Friesian. A synonym of *Hexagona* Poll. ex Fr.

PHYLLODONTIA Karst., Hedw. **22:** 163. 1883.

Type: *P. magnus* Karst.

Invalid: In the sense of Bondartsev and Singer an obligate synonym of *Cerrena* Mich. ex S. F. Gray. Used by them in the *Corioleae* of the *Corioloideae* in the *Polyporaceae*.

PHYLLOPORUS Quél., Fl. Mycol. Fr. 409. 1888.

Lectotype: *P. pelletieri* (Lév.) Quél. according to Singer and Smith, 1946.

An agaric of the *Boletoideae* in the *Agaricales*.

PHYSISPORINUS Karst., Finl. Basidsv. 324. 1889.

Type: *Poria vitrea* Bres.

A segregate of the genus *Poria*; a synonym of *Podoporia* Karst., obligate in the sense of the Donk and Pilát treatments; used by Pilát for the same species placed in *Podoporia* by Donk.

PHYSISPORUS Chev., Flor. Par. **1:** 261. 1836.

Type: *Polyporus obliquus* Pers. ex Fr.

A segregate of *Poria* for species with brown context often put in other polypore genera with brown context such as *Phellinus*, with which it may be cogeneric since *P. obliquus* is considered by some synonymous with *Phellinus igniarius*. If this situation is correct, *Physisporus* would have to replace *Phellinus* because of obligate synonymy. *Physisporus* is rarely used today, when *Poria* segregates are used, since it has been replaced by several genera of Murrill, by *Phellinus*, or by other genera into which brown context species are segregated.

PIPTOPORUS Karst., Soc. Faun. Fl. Febb. Medd. **6:** 9. 1881.

Type: *Polyporus betulinus* Bull. ex Fr.

Used by Donk in the *Polyporeae* of the *Polyporoideae*; by Pilát; by Bondartsev and Singer who placed this with *Cryptoporus* in the *Piptoporeae* of the *Fomitoideae* in the *Polyporaceae*; by Imazeki in the *Piptoporinae* of the *Polyporeae*; used by Pinto-Lopes in the sense of the type in the *Trametoideae*; Kotlaba and Pouzar used this genus in the sense of Pilát.

PLACODES Quél., Ench. Fung. 170. 1886.

Type: *P. flabelliformis* (Scop.).

Invalid: The type is a synonym of *Ganoderma lucidum* (Leyss. ex Fr.) Karst.; this genus is an obligate synonym of *Ganoderma* Karst.

PODOPORIA Karst., Hedw. **31:** 297. 1892.

Type: *P. confluens* Karst.

A segregate of the complex *Poria*, used by Donk for species of

Poria and placed in the *Tyromyceteae* of the *Polyporoideae*; used by Bondartsev and Singer in the *Poroideae* of the *Polyporaceae*.

POGONOMYCES Murr., Torr. Bot. Cl. Bull. **31:** 609. 1904.
Type: *Polyporus hydnoides* Sw. ex Fr.
A segregate of *Trametes*.

POLYPILUS Karst., Rev. Myc. 3(9): 17. 1881.
Type: *Polyporus frondosus* Schrank. ex Fr.
Invalid: An obligate synonym of *Grifola* S. F. Gray. Used by Donk in the *Polyporeae* of the *Polyporoideae*; by Bondartsev and Singer in the *Scutigeraceae* of the *Clavariineae*.

POLYPORELLUS Karst., Soc. Faun. Fl. Fenn. Medd. **5:** 37. 1880.
Type: *Boletus brumalis* Pers.
Not considered distinct from *Polyporus* ss. str. Used by Pilát for species assigned by other workers to *Polyporus* Fr., ss. str., and to *Favolus* Fr.; Pinto-Lopes felt that *Polyporus* Fr. is a *nomen dubium* so uses this genus for *Polyporus* Fr. ss. str., and included as subgenera *Leucoporus*, *Melanopus*, and *Favolus*, in the *Trametoideae*.

POLYPOROLETUS Snell, Mycologia **28:** 467. 1936.
Type: *P. sublividus* Snell.
Considered by Singer, Snell and White (1945) a synonym of *Scutiger* Paul., thus it becomes a synonym of *Albatrellus* S. F. Gray.

POLYPORUS Mich. ex Fr., Syst. Myc. **1:** 341. 1821.
Lectotype: *Polyporus squamosus* Huds. ex Fr., according to Murrill.
Lectotype: *Polyporus tuberaster* Jacq. ex Fr., according to Donk.
Donk placed this genus, including *Favolus* Fr. as a synonym, in the *Polyporeae* of the *Polyporoideae*; Bondartsev and Singer placed this genus in the *Polyporoideae* of the *Polyporaceae* in the sense of Donk; Imazeki used this in the sense of *Albatrellus* in the *Polyporinae* of the *Polyporeae*; Cunningham included most light colored pileate species which are non-perennial in this genus in the *Polyporeae*; Pilát placed most of the species usually assigned here in *Polyporellus*; Overholts and his students and followers used this genus as a repository for all polypores which were non-resupinate, non-perennial, and whose hymenium was not especially configured or whose trama was not especially trametoid; thus he used the genus in the broadest sense of recent workers except those in Sweden who use it in the original sense of Fries including everything except *Daedalea*; Kotlaba and Pouzar used this genus in the sense of Donk. Recently, Singer (1949) has suggested that it is possible that species of this genus, including *Favolus*, are more properly related to *Pleurotus* in the *Tricholomataceae* of the *Agaricales*, to which it should eventually be transferred. If this claim be substantiated the genus *Polyporus*, the family *Polyporaceae* and the order *Polyporales*, as well as numerous other supra generic epithets would become invalid.

POLYPORUS Pers. ex. S. F. Gray. Nat. Arr. Brit. Pl. **1:** 645. 1821.
Type: *P. ramosus* S. F. Gray, a form of *P. sulphureus* Fr.
Invalid: A later homonym of *Polyporus* Mich. ex Fr., 1821.

POLYSTICTOIDES Lazaro, R. Acad. Cienc. Madr. Rev. **14:** 754. 1915–16.

Type: *Polyporus cuticularis* Bull. ex Fr.
Invalid: An obligate synonym of *Inonotus* Karst.

POLYSTICTUS Fr., Nov. Symb. Myc. 54. 1851.
Type: *Polyporus perennis* L. ex Fr.
Invalid: An obligate synonym of *Coltricia* S. F. Gray. Donk uses this genus instead of *Coltricia* and placed it in the *Hymenochaetoideae*; Pilát also used this genus—both authors in the sense of Ames (l.c.)—including *Pelloporus*, *Onnia* and *Coltricia* as synonyms. Pilát used two sections, *Eupolystictus* and *Onnia*, each with one composite species; Bondartsev and Singer used this genus in the sense of *Coltricia* placing it in the *Inonoteae* of the *Fomitoideae* in the *Polyporaceae*; Pinto-Lopes used this genus in the *Xanthochroideae* for species assigned by others to *Coltricia*, *Onnia* and *Inonotus*. See Donk 1949: 142–4 for a discussion of why this genus should be conserved over *Coltricia*.

PORIA Brown ex Adans., Fam. Pl. **2:** 10. 1763.
Type: Not based on a binomial.
Invalid: Pre-Friesian.

PORIA Pers., Neues Mag. Bot. (Roem.) **1:** 109. 1794.
Type: *Polyporus medulla-panis* Jacq. ex Fr.
Invalid: Pre-Friesian.

PORIA Pers. ex S. F. Gray, Nat. Arr. Brit. Pl. **1:** 639. 1821.
Type: *Polyporus vulgaris* Fr.
An emended form of this genus was used by Cunningham for all light or bright colored Porias.

PORIA Pers. ex S. F. Gray, Nat. Arr. Brit. Pl. **1:** 639. 1821.
Lectotype: *P. medulla-panis* S. F. Gray according to Donk, 1949: 103.
Note: Gray spelled this specific epithet *P. medularis*.

PORIA Pers. ex S. F. Gray em. M. C. Cooke, Grev. **14:** 109. 1886.
Lectotype: *Poria unita* (Pers.) M. C. Cooke according to Donk, 1949: 105.

PORIA (Pers.) ex Karst., Rev. Myc. **3**(9)**:** 18. 1881.
Lectotype: *Polyporus ferruginosus* Schrad. ex Fr. according to Donk, 1941: 174.

PORIA Pers. ex Karst. em. M. C. Cooke, Grev. **14:** 109. 1886.
Lectotype: *Polyporus medulla-panis* Pers. according to Donk, 1949: 105.
Invalid: A later homonym of *Poria* Pers. ex S. F. Gray, 1821.
It should be noted that in 1933 Donk considered this a form genus without a type and whose species could well be demonstrated later to be pileate; he placed it as a supplement to the *Polyporoideae*; Pilát used *Poria* (Pers.) Cooke for most of the resupinate polypores not assignable to *Leptoporus* (*Tyromyces*). He divided it into eight sections of which species assigned to four could be transferred to the genera for which the sections were named. He included the following synonyms: *Xylodon*, *Physisporus*, *Physisporinus*, *Trechispora*, *Chaetoporus* and *Ceraporia*. Cunningham included all light colored resupinate species in this genus

in the *Poriae*. Overholts, Lowe, Baxter and other North American students include all resupinate polypores, regardless of tramal color, spore ornamentation, or basidial type, in this genus. These workers did not cite a type in their studies.

PORIUM Adans., Fam. Pl. **2:** 28. 1763.
Type: Not based on a binomial.
Invalid: Pre-Friesian.

POROAURICULA Lloyd, as McGinty, Myc. Writ. **5:** 708. Oct. 1917.
Type: *Laschia intestinalis* Berk.
Stevenson and Cash (1936: 141) state: "This is another of Prof. McGinty's offerings, which Mr. Lloyd never took seriously. If recognized *Poroauricula intestinalis* (Berk.) Lloyd (loc. cit) would become the type species. See *Lashia intestinalis*".

PORODAEDALEA Murr., Torr. Bot. Cl. Bull. **32:** 367. 1905.
Type: *Daedalea pini* Thore ex Fr.
The type is cited in the Elenchus as "Thore" but in the Systema, 1: 336 as "Brot."

PORODINULUS v. Hoehn., Sitzgbr. Akad. Wiss. Wien **123**(1)**:** 84. 1914.
Type: *P. bivalvis* v. Hoehn.
Based on a specimen with an apparent volva; thought by Bondartsev and Singer to be a possible synonym of *Poronidulus*. This could be a misspelling of *Poronidulus*.

PORODISCULUS Murr., N. Am. Fl. **8:** 47. 1907.
Type: *Peziza pendula* Schw.
Imazeki used this in the *Piptoporinae* of the *Polyporeae*.

PORODISCUS Murr., Torr. Bot. Cl. Bull. **30:** 432. 1903.
Type: *Peziza pendula* Schw. ex Fr.
Invalid: A later homonym of *Porodiscus* Grev., 1863.

POROGRAMME (Pat.) Pat., Ess. Taxon. 63. 1900.
Type: *P. grisea* Berk. & Curt.
A genus of the *Thelephoraceae* characterized by sterile structures arranged in the shape of pores.

POROGRAMME Pat. (as section of *Poria*), Soc. Myc. Fr. Bull. **15:** 199. 1899.
Type: *P. dussii* Pat.
See above for note on this in generic form.

POROLASCHIA Pat. in Morat., Journ. Bot. 1887: 231. 1887.
Type: *P. sprucei* (Berk.).
For a discussion of this genus, which is included here because of its porose hymenium, see Singer in Lloydia **8:** 170. 1945, and Lilloa **22:** 738. 1951.

PORONIDULUS Murr., Torr. Bot. Cl. Bull. **31:** 425. 1904.
Type: *Polyporus conchifer* Schw. ex Fr.
Unless the sterile, conchoid structure produced prior to the development of the fruit body is considered a character of generic value this

should be placed with *Coriolus*. Bondartsev and Singer placed this in the *Corioleae* of the *Corioloideae* in the *Polyporaceae*; placed in *Trametes* by Pilát. Brodie has shown that the sterile cups produce conidia which are dispersed by splashing rain drops.

POROPTYCHE Beck., Zbl. Bot. Ges. Wien Verh. **38:** 657. 1887.
Type: *P. candida* Beck.
Invalid: Teratologic. If considered an imperfect state of a polypore it would become a *nomen anamorphosis* and valid in the Fungi Imperfecti.

POROTHELEUM (Fr. ex Fr.) Fr., Syst. Orb. Veg. 80. 1825.
Type: *P. fimbriatum* (Pers. ex Fr.) Fr.
Placed by Bondartsev and Singer in the *Fistulinaceae* of the *Cyphelliineae*. Murrill based the *Porotheliaceae* on this genus. In treating the genera of the "*Cyphellaceae*" Donk discussed this genus at length and decided that it was preoccupied by a genus of Lichens: *Porothelium* Eschw., 1824. The writer (Cooke, 1957) disagreed with this point of view because Eschweiler's genus had a very short life and is no longer used by lichenologists, because there is little likelihood that species of the two genera will ever be confused, and because the two endings are not necessarily subject to confusion, and are not necessarily orthographic variants. The genus is included in this list because of the apparent porose nature of the mature fruit body, and because Lloyd and Overholts made the type species a member of the genus *Poria*.

POSTIA Karst., Rev. Gen. **3**(9)**:** 17. 1881.
Type: *Polyporus borealis* Fr.
Invalid: *Nomen nudum*, and later homonym of *Postia* Boiss. & Blanch., 1875.

PSEUDOFAVOLUS Pat., Ess. Taxon. 80. 1900.
Type: *Hexagona miquelii* Mont.
Included here because of the porose hymenium; see Singer, Lilloa **22:** 269, 283–4. 1951.

PSEUDOFOMES Lazaro, R. Acad. Cienc. Madr. Rev. **14:** 582. 1915–16.
Type: *Polyporus nigricans* Fr.
Not considered distinct from *Phellinus* Quél.

PSEUDOTRAMETES Bond. & Sing. in Singer, Mycologia **36:** 68. 1944.
Type: *P. gibbosa* (Pers.).
Protonym: *Pseudotrametes* Bond. & Sing., Ann. Mycol. **39:** 60. 1941, *nomen nudum*.
A daedaleoid or lenzitoid segregate of *Trametes* Fr. The authors placed this with the *Corioleae* in the *Corioloideae* of the *Polyporaceae*. Returned by Pilát to *Trametes*.

PTYCHOGASTER Corda, Icon. Fung. **2:** 24. 1838.
Type: *P. albus* Corda.
Invalid: Teratologic. If this is considered the imperfect stage of a polypore it becomes a *nomen anamorphosis* and is valid in the Fungi Imperfecti.

PYCNOPORELLUS Murr., Torr. Bot. Cl. Bull. **32:** 489. 1905.
Type: *Polyporus fibrillosus* Karst.
At present not considered distinct from *Inonotus* Karst. Accepted by Kotlaba and Pouzar because the species are not assignable to members of the *Hymenochaetaceae*.

PYCNOPORUS Karst., Rev. Mycol. **3**(9)**:** 18. 1881.
Type: *Polyporus cinnabarinus* Jacq. ex Fr.
Cunningham considered the type a synonym of *P. sanguieus* and made the combination *Coriolus sanguineus* (Fr.) Cunn. As yet unpublished observations of these two fungi in culture do not substantiate this conclusion. Bondartsev and Singer placed this in the *Corioleae* of the *Corioloideae* in the *Polyporaceae*; Pilát placed this genus in *Trametes*; accepted by Kotlaba and Pouzar in the sense of the type.

PYREIUM Paul., Icon. Champ. pl. 5, f. 1–3. 1793.
Type: *Xylostroma giganteum* (Paul.) Tode, according to Murrill.
Invalid: Pre-Friesian; Mycelia Sterilia.

PYROPOLYPORUS Murr., Torr. Bot. Cl. Bull. **30:** 109. 1903.
Type: *Polyporus igniarius* L. ex Fr.
Invalid: An obligate synonym of *Phellinus* Quél.

RIGIDIIPORUS Murr., Torr. Bot. Cl. Bull. **32:** 478. 1905.
Type: *Polyporus micromegas* Mont.

RODWAYA H. &. P. Sydow, Hedw., Beiblatt 40(1)**:** 2. 1901.
Type: *Campbellia infundibuliformis* Cke. & Mass.

ROMMELLIA Murr., Torr. Bot. Cl. Bull. **31:** 338. 1904.
Type: *Polyporus schweinitzii* Fr.
Invalid: An obligate synonym of *Phaeolus*.

SARCOPORIA Karst., Hedw. **33:** 15. 1894.
Type: *S. polyspora* Karst.
A segregate of *Poria* near to or synonymous with *Podoporia* Karst.

SCALARIA Lazaro, R. Acad. Cienc. Madr. Rev. **14:** 741. 1915–16.
Type: *S. fusca* Lazaro.
Probably assignable to one of the perennial genera considered valid here.

SCENIDIUM O. Kuntze, Rev. Gen. Pl. **3:** 515. 1893.
Type: *Polyporus hirtus* Pal. de Beauv. ex Fr.
Not considered distinct from *Favolus* Fr.

SCINDALMA Hill. ex O. Kuntze, Rev. Gen. Pl. **3:** 517. 1893.
Type: *Polyporus igniarius* L. ex Fr.
Invalid: An obligate synonym of *Phellinus* Quél.

SCLERODEPSIS Cooke, Grev. **19:** 49. 1890–91.
Type: *Trametes colliculosa* Berk.
A segregate of, and probably not distinct from, *Trametes* Fr.

SCUTIGER Paul., Icon. Champ., pl. 31, f. 1–3. 1793.
Type: *S. tuberosus* Paul.
Invalid: Pre-Friesian.

SCUTIGER Paul. ex Murr., Torr. Bot. Cl. Bull. **30:** 428. 1903.
Type: *S. tuberosus* Paul.
Considered synonymous with *Albatrellus* S. F. Gray, although used by Donk and placed in the *Polyporeae* of the *Polyporoideae*; Bondartsev and Singer used this in the *Scutigeraceae* of the *Clavariineae*. Since this genus is synonymous with *Albatrellus* it may be desirable to change the family name. Kotlaba and Pouzar maintain this genus distinct from *Albatrellus* because of the presence of clamp connections in the type species.

SERDA Adans., Fam. Pl. **2:** 11. 1763.
Type: Daedalea sepiaria Fr.
Invalid: Pre-Friesian; an obligate synonym of *Gleoeophyllum* Karst.

SERPULA Pers. ex S. F. Gray, Nat. Arr. Brit. Pl. **1:** 637. 1821.
Type: *Serpula destruens* Pers. ex S. F. Gray which is *Merulius lacrimans* Fr. or *Serpula lacrimans* (Fr.) Karst.
A member of the *Coniophora* series although included in *Merulius* by Burt, Cunningham and most workers, but see Cooke (1957).

SERPULA Pers. ex Karst., Soc. Faun. Fl. Fenn. Medd. **11:** (21). 1884.
Type: *Merulius lacrimans* Schumm. ex Fr.
Invalid: An obligate synonym of *Serpula* Pers. ex S. F. Gray.

SESIA Adans., Fam. Pl. **2:** 10. 1763.
Type: *Merulius lacrimans* Schum. ex Fr. but not as a binomial.
Invalid: Pre-Friesian; an obligate synonym of *Serpula* Pers. ex S. F. Gray.

SESIA Adans. ex O. Kuntze, Rev. Gen. Pl. **2:** 869. 1891.
Type: *S. byssina* Scop. ex O. Kuntze which is *Merulius lacrimans* Fr.
Invalid: An obligate synonym of *Serpula* Pers. ex S. F. Gray.

SISTOTREMA Pers. ex Fr., Syst. Myc. **1:** 426. 1821.
Type: *S. confluens* Pers. ex Fr.
Considered a polypore by Pilát intermediate between the Hydnums and *Heteroporus*. Bondartsev and Singer used *Sistotrema* in the broadest sense, that of an early paper of Rogers (1935), and included it in the *Corticiaceae* of the *Corticiineae*, for the several corticioid species of *Poria*. See *Cristella*.

SKELETOCUTIS Kotlaba and Pouzar, Česká Mykologie **12:** 103, 104. 1958.
Type: *Polyporus amorphus* Fr. ex Fr.
A segregate of *Gloeoporus* in the earlier sense of the authors.

SPONGIOIDES Lazaro, R. Acad. Cienc. Madr. Rev. **14:** 574. 1915–16.
Type: *Boletus cryptarum* Bolt.
Probably a segregate of *Poria* not at present considered distinct.

SPONGIOSUS Torrend, Broteria, Ser. Bot. **21:** 39. 1923.
Type: Section *Spongiosus* of Lloyd's Stipitate Polypores.
See above notes on Torrend's genera.

SPONGIPELLIS Pat., Hym. Eur. 137. 1887.
Type: *S. spumeus* (Fr.).
Bondartsev and Singer placed this in the *Tyromycetoideae* of the *Polyporaceae*; accepted by Kotlaba and Pouzar in the sense of the type.

SPONGIPORUS Murr., Torr. Bot. Cl. Bull. **32:** 474. 1905.
Type: *Polyporus leucospongia* Cooke & Harkness.

STRIGLIA Adans., Fam. Pl. **2:** 10. 1763.
Type: *Daedalea aurea* Fr., but not as a binomial.
Invalid: Pre-Friesian.

STRIGLIA Adans. ex O. Kuntze, Rev. Gen. Pl. **2:** 871. 1891.
Type: *Daedalea aurea* Batt. ex Fr.
Invalid: A later homonym of *Strilia* S. F. Gray which is *Coltricia* S. F. Gray.

STRILIA Mich. ex S. F. Gray, Nat. Arr. Brit. Pl. **1:** 645. 1821.
Type: *Boletus cinnamomeus* Jacq., according to Donk, 1950: 4.
A synonym of *Coltricia* S. F. Gray. The spelling *Striglia* used by Gray in connection with this genus was an attempt to give a common name.

SULPHURINA Pilát ex Pilát, Acta Mus. nat. Prag. B 9(2):109. 1953.
Type: *S. sulphurea* (Quél.).
Protonym: *Sulphurina* Pilát, Atlas III. Polyporaceae 1:473. 1942. (*Nomen nudum*, no Latin diagnosis.)
A segregate of *Sistotrema* intermediate between the *Hydnaceae* and the *Thelephoraceae* according to Pilát; used for certain corticioid Porias.

THELEPORUS Fr., Hornsch. Skand. Beitr. **2:** 338. 1847.
Type: *T. cretaceus* Fr.
A thelephoraceous group related to, if not identical with, *Porogramme*.

TILOTUS Kalchbr., Grev. **9:** 137. 1881.
Type: *T. lenzitiformis* Kalchbr.
Invalid: Orthographic variant and later homonym of *Tylotus* J. Agd., 1876.

TINCTOPORIA Murr., N. Am. Fl. **9:** 14. 1907.
Type: *Poria fuligo* B. & Br. var. *aurantiotingens* Ell. & Macbr.
Apparently based on the wood staining properties of the type species, a segregate of *Poria* assigned to *Porogramme* by Lowe (1958).

TOMENTIFOLIUM Murr., Journ. Mycol. **9:** 94. 1903.
Type: *Tilotus lenzitiformis* Kalchbr.

TOMOPHAGUS Murr., Torreya **5:** 197. 1905.
Type: *Polyporus colossus* Fr.

TRACHYDERMA Imazeki, Bull. Govt. For. Expt. Sta. **57**:97. 1952.
Type: *T. tsunodae* (Yasuda) Imazeki.
A segregate of *Ganoderma* or *Elfvingia* in the *Ganodermataceae*.

TRAMETELLA Pinto-Lopes, Mem. Soc. Broteriana **8**: 164. 1952.
Type: *T. hispida* (Bagl.) Fr.
Placed by Pinto-Lopes in the *Phaeochroideae*.

TRAMETES Fr., Fl. Scand. 339. 1835.
Type: *Daedalea suaveolens* Fr.
Included by Donk in the *Daedaleae* of the *Polyporoideae*; Pilát included in this genus all light context genera with pale trama such as *Antrodia*, *Coriolellus*, *Coriolus*, *Cyclomycetella*, *Cerrena*, *Daedalea*, *Lenzites*, *Irpiciporus*, *Daedaleopsis*, *Hexagona*, *Pogonomyces*, *Hirshioporus*, *Poronidulus* and *Irpex*. Bondartsev and Singer included this in the *Corioleae* of the *Corioloideae* in the *Polyporaceae* only in the sense of the type; Imazeki used this in the *Trametinae* of the *Polyporeae*; Cunningham used this probably in the *Fomiteae* since he considered this genus the brown counterpart of *Coriolus* in the *Polyporeae*, the type he chose was *T. hispida* (Bagl.) Fr.; Pinto-Lopes used this in the *Trametoideae* largely in the same way that Pilát used it; Kotlaba and Pouzar used this genus in the sense of the type but with the addition of some species usually placed in *Coriolus*; Overholts used this genus in a somewhat restricted sense as described above.

TRECHISPORA Karst., Hedw. **29**: 147. 1890.
Type: *T. onusta* Karst.
A segregate of *Poria* and *Corticium* for species with urnigera-type basidia assigned to *Sistotrema* by Rogers (1935). Bondartsev and Singer included in this genus species assignable to *Phlebiella* Karst.

TRICHAPTUM Murr., Torr. Bot. Cl. Bull. **31**: 608. 1904.
Type: *Polyporus trichomallus* Berk. & Mont.

TRUNCOSPORA Pilát ex Pilát, Acta Mus. Nat. Prag. B. 9(2):108, 1953.
Type: *T. ochroleuca* (Berk.).
Protonym: *Truncospora* Pilát, Atlas III, Polyporaceae 1:365. 1941. *Nomen nudum* (no Latin diagnosis).
Erected to include polyporoid and fomitoid species with hyaline, thick-walled, truncate spores. *Ungulina* is typified by the same species and is considered valid.

TUBERASTER Boccone, Museodi Fisica e di Esperienza, Venice. 1697.
Type: *P. tuberaster* Fr., but not as a binomial.
Invalid: Pre-Friesian; not distinct from *Polyporus* Fr., ss. str.

TYROMYCES Karst., Rev. Myc. **3**(9): 17. 1881.
Type: *Polyporus chioneus* Fr.
In addition to including several segregates of *Poria*, Donk added *Laetiporus* Murr. and *Spongiporus* Murr. to this genus, on which he based the *Tyromyceteae* of the *Polyporoideae*; Bondartsev and Singer placed this in the *Tyromycetoideae* of the *Polyporaceae*; Imazeki used this in the *Tyromycetinae* of the *Polyporeae*; Kotlaba and Pouzar accept this genus in the sense of the type, but indicate that on the basis of hyphal systems it is a polymorphic genus.

UNDERWOODINA O. Kuntze, Rev. Gen. Pl. **3**(2): 538. 1898.
Type: *Bizzozeriella basicystis* O. Kuntze.
Erected to replace *Aschersonia* Berk. & Mont. 1844, non Endl. 1842.

UNGULARIA Lazaro, R. Acad. Cienc. Madr. Rev. **14:** 668. 1915–16.
Type: *Polyporus betulinus* Bull. ex Fr.
Invalid: An obligate synonym of *Piptoporus* Karst.

UNGULINA Pat., Cat. Tun. 48. 1897.
Type: *Polyporus ochroleucus* Berk.
The type was made the type of the genus *Truncospora* by Pilát although this generic epithet is a *later homonym;* it includes species assignable to a number of genera considered valid in this list; accepted in the sense of the type as a replacement for the invalid *Truncospora* by Kotlaba and Pouzar.

VARARIA (Karst.) Karst., Bidr. Känned. Finl. Nat. Folk. **62:** 96. 1903.
Type: *Radulum investiens* Schw.
Used in the form of its synonym *Astrostromella* by Bondartsev and Singer in the *Corticiaceae* of the *Corticiineae* for species of *Poria*. Donk based the subfamily of the *Aphyllophoraceae*, *Vararioideae*, on this genus.

VOLVOPOLYPORUS Lloyd, as McGinty, Myc. Writ. **3:** 444. 1909.
Type: *Polyporus peronatus* Schulz.
Based on an old illustration. Stevenson and Cash (1936: 148) report: "Specimens not represented in the Lloyd Herbarium. This 'new genus' based on *Polyporus peronatus* Schulz. is one of Mr. Lloyd's pleasantries and can be ignored, except to note that it has been recorded by Saccardo (Syll. Fung. **21:** 282. 1912)."

WHITFORDIA Murr., Torr. Bot. Cl. Bull. **35:** 407. 1908.
Type: *Fomes warburgianus* P. Henn.

XANTHOCHROUS Pat., Cat. Tun. 51. 1897.
Type: *Polyporus perennis* L. ex Fr.
Invalid: An obligate synonym of *Coltricia* S. F. Gray as well as containing a number of brown context species belonging to other genera; Pinto-Lopes used this in the *Xanthochroideae* for species of *Inonotus*.

XANTHOPORIA Murr., Mycologia **8:** 56. 1916.
Type: *Mucronoporus andersonii* Ell. & Ev.
A very characteristic segregate of the brown context species of *Poria*.

XEROTINUS Richenb., Consp. Regni Veg. 14. 1828.
Type: *X. afer* Fr.
Erected in a list to replace *Xerotus* Fr. Singer (Lilloa **22:** 744. 1951) indicates that the type is a species of *Gloeophyllum*, while Murrill in North American Flora indicates that the type is stipitate. If Singer is correct *Xerotinus* will replace *Gloeophyllum*.

XEROTUS Fr., Elench. Fung. 48. 1828.
Type: *X. afer* Fr.
Invalid: A later homonym of *Xerotus* R. Br., 1810, and a synonym of *Xerotes* Fr., which Murrill considered an orthographic variant.

XYLODON Ehrenb., Sylvae Mycol. Berol. 30. 1818.
Type: No species listed, used as a descriptive term under *Sistotrema candida*.
Invalid: Pre-Friesian.

XYLODON (Ehr.) Karst., Soc. Fann. Fl. Fenn. Medd. **2:** 31. 1881.
Type: *Irpex paradoxus* Fr.
Not considered distinct from *Irpex* Fr. if segregated from *Poria*. Bondartsev and Singer considered the type a synonym of *Poria mucida* Pers., thus a synonym of *Poria versipora*, and placed this genus in the *Poroideae* of the *Polyporaceae*.

XYLODON Pers. ex S. F. Gray, Nat. Arr. Brit. Pl. **1:** 649. 1821.
Type: *Sistotrema quercinum* (Pers.) Pers.
Following Donk (Taxon **5:** 113, 1956) in this choice of a type species for this genus would reverse the conclusion of Singer (Mycologia **36:** 66, 1944). See Donk's paper for the complete discussion of this point. This leaves the species treated by Bondartsev (1953) in this genus without a generic name.

XYLODON Ehrenb. ex O. Kuntze, Rev. Gen. Pl. **3**(2): 540. 1898.
Type: *X. candidus* Ehrenb.
Invalid: A later homonym of *Xylodon* (Ehrenb.) Karst.

XYLOMETRON Paul., Comp. Icon. Pl. 3, f. 1–4, 1793.
Type: *X. lobatum* Paul.
Invalid: Pre-Friesian.

XYLOMYZON Pers., Myc. Eur. **2:** 26. 1825.
Type: *Merulius destruens* Pers. which is *Merulius lacrimans* Fr.
Invalid: An obligate synonym of *Serpula* Pers. ex S. F. Gray.

XYLOPHAGUS Link, Mag. d. ges. naturf. Freunde Berlin **3:** 38. 1809.
Type: *X. lacrimans* (Wulf.) Lk.
Invalid: Pre-Friesian; an obligate synonym of *Serpula* Pers. ex S. F. Gray.

XYLOPILUS Karst., Bidr. Finl. Nat. Folk **37:** ix. 1879.
Type: *X. crassus* (Fr.) Karst.

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The Structure of the Female Inflorescence and Its Taxonomic Value in the Genus Trichocolea

(Hepaticae)

Raymond E. Hatcher
(*Department of Biological Sciences, University of Cincinnati, Cincinnati, Ohio*)

The structure and development of the female fruiting structure in *Trichocolea* has for a long time been the subject of considerable disagreement among hepaticologists. While most investigators have agreed that certain differences in structure occur, opinions have differed widely as to their nature and applicability to the taxonomy of the genus.

An examination of the fruiting structure of a number of the species has revealed three recognizably distinct types or patterns of development within the genus. The one most widely distributed among the leafy Hepaticae is that found in *Trichocolea tomentosa*. In this species there are three series of bracts (figs. 1A, 3A) and bracteoles which are distinguished from normal leaves (fig. 1K) and underleaves principally on the basis of their larger size. These bracts and bracteoles subtend a large, inflated perianth (figs. 1B, 3B) the mouth of which is broad and dissected into a number of triangular segments with ciliate margins. The outer or exposed surface of the perianth is more or less densely clothed with short, simple or branched paraphyllia (fig. 1F) and occasional paraphyllia may be found on the inner surface.

Following fertilization of one of the archegonia clustered at the apex of the stem, the young sporphyte grows and becomes differentiated into a foot, seta, and capsule. The foot penetrates into the stem tissue below the venter and the tip finally reaches a position at about the level of the outermost series of bracts. During this period of development of the young sporophyte, the surrounding tissue of the archegonial venter also undergoes growth and expansion and continues to enclose the seta and capsule. This increase in size of the venter is facilitated by cell division in, mostly, two planes allowing for an increase in length and circumference and resulting in a large, broadly ovoid, relatively thin-walled "calyptra" (fig. 1C) surmounted by the neck of the old archegonium. It is apparent also that a narrow band of stem tissue surrounding the base of the venter becomes meristematic (fig. 3P). This is indicated by the fact that the sterile archegonia (figs. 1E, 3E) surrounding the young venter in its early stages of development appear, in later stages, to have been uplifted onto the surface of the "calyptra." Such a condition would not be possible if the venter alone had been involved in the formation of the calyptra for, if the latter were true, the sterile archegonia would have been narrowly restricted to the angle formed between the calyptra and the insertion of the perianth. An examination of the "calyptra" in Figure 1C indicates that that portion derived from the tissue of the venter occupies the upper half or dome of the calyptra while the lower half is composed of stem tissue. As was mentioned above, this type of inflorescence is common among the leafy Hepaticae and may be found in such genera

as *Herberta*, *Herpocladium*, *Ptilidium*, *Lepidozia*, and many others. Knapp (1930) described this calyptra in considerable detail and referred to it as a "*Sprosskalyptra*" or *shoot calyptra*.

Because of its relative lack of specialization and its wide occurrence in many unrelated genera of modern leafy Hepaticae, I consider this type of fruiting structure to be the most primitive of the three found in the genus *Trichocolea*. The two types described below comprise distinct and divergent lines evolved from the unspecialized type found in *T. tomentosa* and result in the formation of perigynia. According to Evans (1939), a perigynium is composed of a sheath of cauline tissue surrounding the developing embryo.

One of these divergent lines of development is found in *Trichocolea lanata* (figs. 4, 6). Here the young sporophyte proceeds to burrow into the tissue of the stem below the venter of the archegonium as it does in *T. tomentosa*, but, unlike the sporophyte of this latter species, that of *T. lanata* continues to grow downward through the stem tissue for a considerable distance below the outermost series of bracts and bracteoles thus forming a hollow cylinder of stem tissue (fig. 6L) in which the sporophyte matures. A perianth (figs. 4B, 6B) is present at the summit of this cylinder of stem tissue and is similar to that of *T. tomentosa* except that it is usually more deeply divided than in the latter species and paraphyllia are absent from its surfaces. Within the perianth, a dome-shaped shoot calyptra (fig. 6C) develops. Again, as in *T. tomentosa*, a band of meristematic tissue forms around the base of the archegonial venter (fig. 4P). In this species, however, it appears that the tissue of the venter undergoes very little growth, and the band of meristematic stem tissue is responsible for the formation of the bulk of the calyptra. This is indicated by the fact that the mature calyptra is several cell layers in thickness and that sterile archegonia (fig. 6E) are scattered over the whole of its surface. As may be seen by comparing Figures 1 and 6 and Figures 3 and 4, all structures found in *T. tomentosa* are also present in *T. lanata*. The differences between the fruiting structures of the two species results from the action of the young developing sporophyte, which, in *T. lanata*, penetrates deeply into and hollows out an extensive cylinder of stem tissue, and in the "calyptra," which, in this species is composed almost entirely of stem tissue, growth of the venter having been greatly restricted.

The pattern of development of the perigynium in *Trichocolea lanata* is rare among the leafy Hepaticae and has been found, thus far, only in the genus *Lepidolaena* (*L. magellanica* (Lam.) Schiffn., *L. Ljungneri* Herz. and *L. Weindorferi* Herz.), and *Schistochila* (S. *balfouriana* (Tayl.) St., *S. kirkiana* St., *S. appendiculata* (Hook.) St., *S. glaucescens* (Hook.) St., etc.).

The most striking departure from the pattern of development in *T. tomentosa* is that of the third type found in the fruiting structure of *T. tomentella* (figs. 2, 5). In this species, fertilization and the beginning of development of the young sporophyte apparently stimulate the formation of a broad meristematic zone of stem tissue between the base of the fertile archegonium and the point of insertion of the innermost series of bracts (fig. 5P). Growth of this ring-shaped zone of meristematic tissue subsequently results in the formation of a long,

hollow, thick-walled, club-shaped perigynium (fig. 2M) which encloses the developing sporophyte. This structure is densely clothed with simple or branched paraphyllia and the sterile archegonia (fig. 2E) are found scattered about the region of the apex. No tissue derived from the venter of the fertilized archegonium can be distinguished here and it is apparent that the venter contributed little toward the formation of the perigynium. A perianth, as such, is entirely absent in this species, but careful examination has revealed a few vestigial, leaf-like structures (fig. 2N) scattered over the surface of the mature perigynium. These probably represent the remnants of a very young perianth which had begun to form before fertilization had taken place and whose development was curtailed by the onset of growth in the meristematic zone described above. Subsequent growth of the perigynium would result in the foliar segments comprising the perianth being pulled apart and differential rates of growth within the tissue of the perigynium would account for the scattered distribution of the individual segments. As may be seen in Figure 2H, the foot of the mature sporophyte penetrates only a short distance into the tissue of the stem, its tip reaching a point only slightly below the point of insertion of the innermost series of bracts.

The term coelocaule has been applied by Goebel (1930) and Knapp (1930) to the types of perigynia found in *Trichocolea lanata* and *T. tomentella*. It is apparent, however, that, in so far as the origin and development of the fruiting structures of these two species are quite different, specific terms are needed in order to delimit them satisfactorily. Since the mature structure of the coelocaule in *T. tomentella* is uplifted above the level of the bracts and bracteoles, this structure is here designated as an *epicoelocaule*. That of *T. lanata*, in which the coelocaule if formed at the same level and below the bracts and is thus covered by the bracts and bracteoles may be referred to as a *cryptocoelocaule*.

As was mentioned earlier, considerable confusion and disagreement has surrounded the nature of the fruiting structure and the value of observed structural differences as they might apply to the taxonomy of the genus. The nature of the structures has been discussed above and it is now only necessary to consider their taxonomic value. A full discussion of the taxonomic history of *Trichocolea* appears in a previous paper, (Hatcher, 1957), but a brief summary is included here.

Gottsche (1864) was the first to recognize differences between the fruiting structures of *T. tomentella* and *T. tomentosa*. On the basis of

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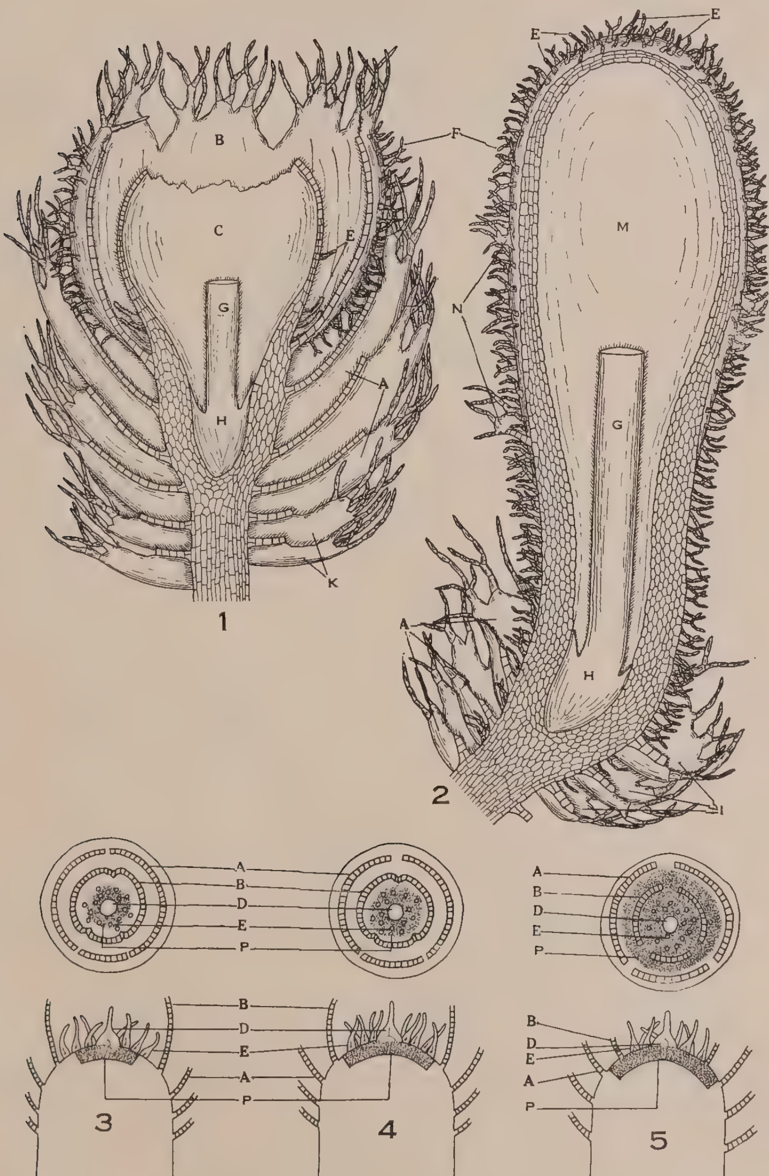
EXPLANATION OF FIGURES

FIGS. 1 and 3. *Trichocolea tomentosa;* FIGS. 2 and 5. *Trichocolea tomentella;* FIG. 4. *Trichocolea lanata*. FIGS. 1–2. Median longitudinal section of the mature female fruiting structure (X 20). FIGS. 3–5. Diagrammatic representation of the fertile stem tip showing arrangement and spatial relationship of structures. A. Bracts; B. Perianth; C. Shoot Calyptra; D. Fertilized archegonium; E. Sterile archegonia; F. Paraphyllia; G. Sporophyte stalk; H. Sporophyte foot; I. Bracteoles; K. Leaves; M. Epicoelocaule; N. Scattered perianth segments; P. Meristematic region. Fig. 1 drawn from material from Costa Rica collected by P. C. Standley, no. 48,165 (Hb. Herzog). Fig. 2 drawn from material collected by the author in Cheboygan Co., Michigan.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these differences, he subdivided the genus *Trichocolea* into two sections—Section *Hirtiflora* in which the calyptra is fused with and surrounded by the bracts and bracteoles, and Section *Laeviflora* in which the calyptra is smooth and free. Section Hirtiflora was represented by *T. tomentella*, *T. mollissima* and *T. lanata*. Section *Laeviflora* was represented by *T. tomentosa*. Lindberg (1875) raised Gottsche's Section *Laeviflora* to generic rank and gave to it the name *Leiomitra*. Spruce (1885) employed the name *Leiomitra* for his South American species, but with stated reservations and, later, in 1893, he reduced

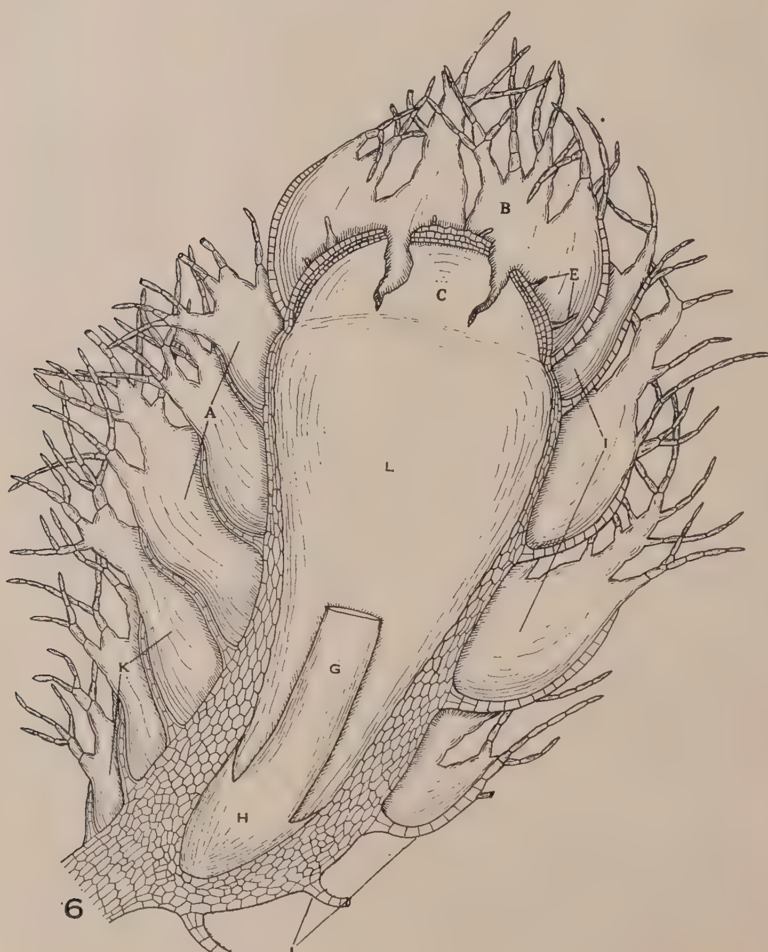

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FIG. 6. *Trichocolea lanata*. Median longitudinal section of the mature female fruiting structure (X 20). A. Bracts; B. Perianth; C. Shoot calyptra; E. Sterile archegonia; G. Sporophyte stalk; H. Sporophyte foot; I. Bracteoles; J. Underleaves; K. Leaves; L. Cryptocoelocaule. Fig. 6 drawn from material collected by the author near Auckland, New Zealand.

Leiomitra to a subgenus of *Trichocolea*. Stephani (1909–12) considered that differences between the fruiting structure of *T. tomentella* and *T. tomentosa* were too slight to merit any subdivision of the genus and Knapp (1930) agreed with Stephani. Knapp described the fruiting structures of *T. tomentella* and *T. tomentosa* in considerable detail, but failed to note the presence of a perianth in *T. tomentosa*.

While three distinct types of fruiting structures are found in the genus *Trichocolea*, no vegetative differences have been found to correlate with them and since many of the species, and particularly those from the tropics, are known to fruit only rarely if at all, any attempt to segregate the species into more than one genus on the basis of type of fructification would, I believe, be unsatisfactory and generally inapplicable. The subdivision of *Trichocolea* into sections appears feasible, however, but before going further, it is necessary to reconsider Gottsche's original subdivisions. Gottsche's explanation of his Section *Laeviflora* (*T. tomentosa*) is sufficiently clear and delimited that it may be retained, but his Section *Hirtiflora*, including both those species bearing an epicoelocaule and those bearing a cryptocoelocaule, leads to confusion. According to the International Code of Botanical Nomenclature (1956), the section including the type species of the correct name of the genus to which it is assigned repeats that name unaltered as its epithet. Thus, since *T. tomentella*, producing an epicoelocaule, is the type species of the genus *Trichocolea*, I should like to propose the Section *Trichocolea* for all those species which form this type of coelocaule. *T. tomentella* would represent the type of this section. For those species, like *T. lanata*, which produce a cryptocoelocaule, the Section *Cryptocaulia* may be established, with *T. lanata* as its type.

Thus the species of *Trichocolea* for which the type of fruiting structure has been established may be classified as follows:

TRICHOCOLEA sect. LAEVIFLORA Gott. (cum perianthio et calyptra caulis)
- *T. tomentosa* (Sw.) Gott. (tropical America)
- *T. Elliottii* St. (tropical and temperate South America and the Caribbean area)
- *T. paraphyllina* (Sphr.) St. (tropical America)

TRICHOCOLEA sect. **Trichocolea** sect. nov. (sine perianthio cum epicoelocaule)
- *T. tomentella* (Ehrh.) Dum. (Circumboreal)
- *T. mollissima* (Hook. & Tayl.) St. (New Zealand)
- *T. australis* St. (New Zealand)

TRICHOCOLEA sect. **Cryptocaulia** sect. nov. (cum perianthio et cryptocoelocaule)
- *T. lanata* (Hooker) Nees (New Zealand)

Following is a list of the species of *Trichocolea* in South America (Hatcher, 1957) and New Zealand (Hatcher, 1958) for which the type of female fruiting structure has not yet been established:

SOUTH AMERICA

Trichocolea filicaulis St.	*T. brevifissa* St.
T. floccosa Herzog & R. Hatcher	*T. elegans* Lehm.
T. Sprucei St.	*T. robusta* St.
T. flaccida (Spr.) Jack & St.	*T. argentea* Herzog
T. Uleana St.	

NEW ZEALAND

T. julacea R. Hatcher

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I should like to express my appreciation to Dr. Margaret Fulford and Miss Jane Taylor for their kindness in reading the manuscript.

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ERRATUM

Pollen Grain Morphology and Its Taxonomic Significance in the Amherstieae, Cynometreae, and Sclerolobieae (Caesalpiniaceae) with Special Reference to American Genera by *Sister M. Veronica Fasbender, O.S.B.*, Lloydia 22(2): 107–162.

Figure 15 is a large scatter diagram which was made to fit on facing pages. Unfortunately the two pages were erroneously placed in the article. The first half of the diagram should be on p. 158 and the second half which has the title, fig. 15, on p. 159. The legend for fig. 15 thus applies to the entire diagram. The legend given to the diagram on p. 159, "Fig. 15a See *Gossweilerondedron* . . . is to be entirely disregarded.

Species of Aschersonia (Sphaeropsidales)[1]

E. B. Mains

Petch (1921) has given a detailed account of species of Aschersonia in his publication concerning the "Genera Hypocrella and Aschersonia". They are parasites of white flies (Aleyrodidae) and scale insects (Coccidae). Aschersonia is the conidial stage of Hypocrella. Most of the species commonly occur in the Ashersonia condition and perithecia are rarely collected. Types of a number of the species have been made available for study from the Farlow Herbarium by I. Mackenzie Lamb, from the Herbarium of the New York Botanical Garden by Clark T. Rogerson, from Mycological Collections, U. S. Bur. Pl. Ind. by John A. Stevenson, from the Herbarium of the Florida Agr. Exp. Sta. by Erdman West and from the Naturhistoriska Riksmuseet of Sweden by T. E. Hasselrot. The information obtained is presented here.

Aschersonia cubensis Berk. & Curtis. Jour. Linn. Soc. **10:** 351. 1869.

This species was described as No. 557 in Fungi Cubenses and was based on a collection from Cuba by C. Wright, No. 427. There is a specimen from the type collection in the Curtis collection of the Farlow Herbarium and another in the general collection. The stromata (fig. 1) are hemispherical, 1–2 mm wide, light yellowish brown and somewhat pruinose, with one or two large pycnidial orifices. The pycnidia are large, irregular to labrinthiform with wide openings. The pycnidiospores (fig. 2) are broadly fusoid, $10–12 \times 3–4\ \mu$. Paraphyses do not occur.

This is a common species of the American tropics. According to Petch (1921) it is the Aschersonia stage of *Hypocrella epiphylla* (Massee) Sacc., the type of that species containing immature pycnidia. However he found that a collection of *A. cubensis* made by Thaxter in Trinidad had mature perithecia. Two of Thaxter's collections from Trinidad in the Farlow Herbarium Nos. 3974 and 3976 determined by Petch as *Aschersonia cubensis* have perithecia of *Hypocrella epiphylla*. The perithecial stage however, is very rarely produced. The hemispherical stromata, few large pycnidia and broad fusoid spores characterize the species.

Aschersonia amazonica P. Henn. Hedwigia **43:** 388. 1904.

Aschersonia amazonica was described by Hennings from a collection by E. Ule, No. 3208 on leaves of Bignoniaceae from Rio Amazonas, Iquitos, Peru. The type in the herbarium of the Naturhistoriska Riksmuseet of Sweden has been studied. The stromata are hemisperhical, 0.5–1 mm, brownish or yellowish, pruinose and have one large central orifice. The pycnidia are cupshaped to broadly ovoid with large openings, $300–500\ \mu$, and the pycnidiospores are broadly

[1]Paper from The Herbarium and Department of Botany, University of Michigan, Ann Arbor, Michigan.

fusoid, 10–12×3–4 μ, and guttate. Paraphyses were not seen. It has stromata, pycnidia, and spores similar to those of *A. cubensis* and, as Petch (1921) has concluded, is that species.

ASCHERSONIA MARGINATA Ellis & Ever. Bul. Torrey Bot. Club **22:** 436. 1895.

This species was described from a collection by A. A. Heller No. 1945 on leaves of ***Psidium*** from the Island of Oahu, Hawaii. It was distributed in Heller's Plants of the Hawaiian Islands and specimens have been studied from the Farlow Herbarium, New York Botanical Garden and Mycological Collections, U. S. Bur. Pl. Ind. The stromata (fig. 3) are hemispherical or pulvinate, 1–2.5 mm wide and black. The orifices of the pycnidia are scattered and medium size. The pycnidia are irregular and the pycnidiospores (fig. 4) are fusoid, 5–8(10)×1.5–2 μ with acute ends. Paraphyses were not seen.

Petch (1921) states that this is on a Lecanium and that it is the pycnidial stage of *Hypocrella reineckiana* P. Henn. of the eastern hemisphere. *Hypocrella palmae* of the western hemisphere is a very similar species.

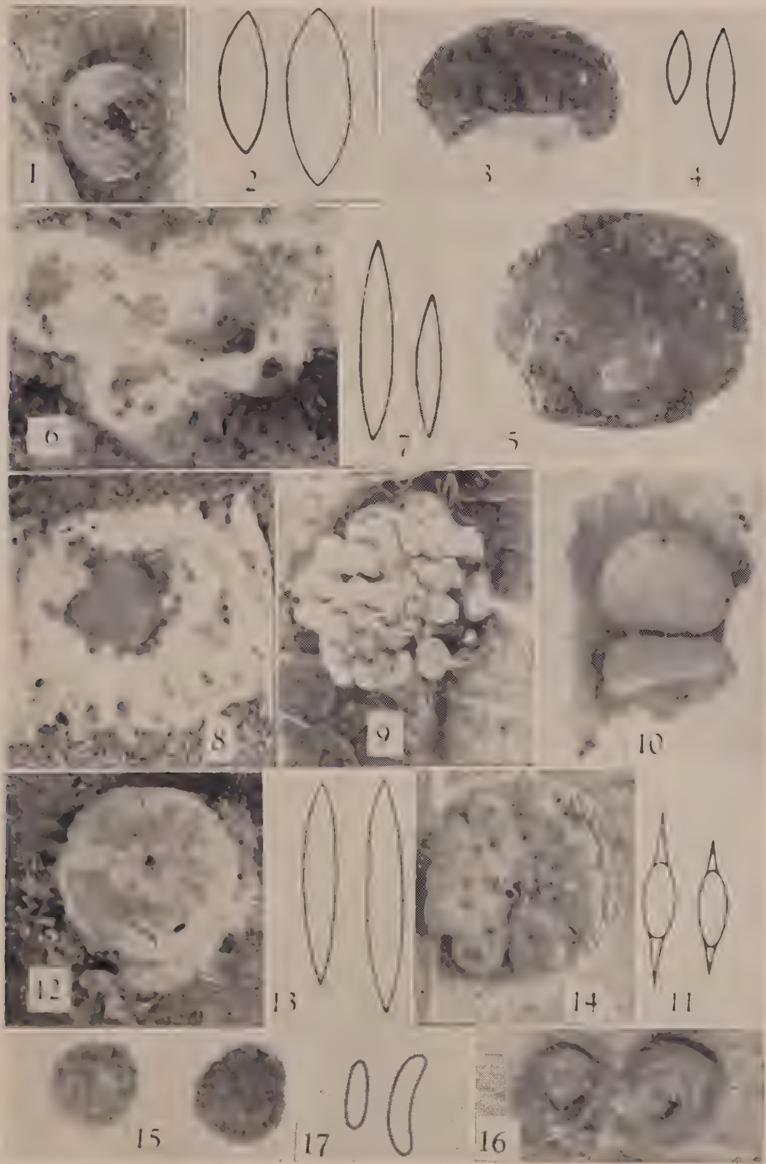
ASCHERSONIA PISIFORMIS Pat. Bul. Soc. Myc. France **22:** 59. 1906.

This species was described from a collection made by Seurat on Cocci at Taravao in Tahiti. A part of the type collection from the Farlow Herbarium No. 4002 has been studied. The stromata (fig. 5) are hemispherical to subgloboid, 2–3 mm wide and black. The orifices of the pycnidia are inconspicuous. The pycnidiospores are fusoid 6–8×1.5–2 μ with acute ends. Paraphyses are lacking. The stromata are more globoid than those of *A. marginata* but as Petch (1921) has concluded it is conspecific.

ASCHERSONIA ALEYRODIS Webber, U. S. Dept. Agr. Div. Veg. Phys. Path. Bul. **13:** 20. 1897.

Webber first reported (1894) this fungus as *Aschersonia tahitensis* Mont. on white fly. It was sent to Patouillard who compared it with type material of that species and concluded that it was distinct. In publishing *A. aleyrodis* as a new species, Webber stated that it occurred in Florida without citing specimens. In his discussion he reported it from Barlow, Crescent City, Gainesville, Myers and Manatee, Florida. Specimens collected by Webber at Manatee in 1896 occur in the Farlow Herbarium and in Mycological Collections, U. S. Bur. Pl. Ind. The stromata (fig. 6) are scutate to flattened pulvinate, 1–3 mm wide, white with wide thin translucent hypothalli. The orifices of the pycnidia are wide, circular to oval, scattered or in a peripheral circle. The stromata are more or less covered by an orange pycnidial exudate (fig. 6). The pycnidia are ovoid, 300–400×250–300 μ with wide openings. The pycnidiospores (fig. 7) are fusoid, 10–16×1.5–2 μ with acute ends. The paraphyses are filiform, 75–150 μ long.

This is a very common species on white fly, especially on citrus in the western hemisphere. It is very similar to *Aschersonia placenta* Berk. & Br. of the eastern hemisphere. Petch (1921) distinguishes the species mostly on length of the paraphyses which he gives as 40–80 μ for *A. placenta* and 65–100 μ for *A. aleyrodis*. *A. placenta* is considered



FIGS. 1 and 2. *Aschersonia cubensis*, type; 1, stroma ×10; 2, spores ×2000. FIGS. 3 and 4, *A. marginata*, type; 3, stroma ×10; 4, spores ×2000. FIG. 5, *A. pisiformis*, type, stroma ×10. FIGS. 6 and 7, *A. aleyrodis*, Manatee, Fla. Webber; 6, stromata ×10; 7, spores ×2000. FIG. 8, *A. goldiana*, type, stroma ×10. FIG. 9, *A. caespiticia*, type, stroma ×10. FIGS. 10 and 11, *A. basicystis*, type; 10, one and a half stromata ×10; 11, spores ×2000. FIGS. 12 and 13, *A. flavo-citrina*, type; 12, stroma ×10; 13, spores ×2000. FIG. 14, *A. crenulata*, type, stroma ×10. FIG. 15, *A. badia*, type, stromata ×10. FIGS. 16 and 17, *A. intermedia*, type; 16, stromata ×10; 17 spores ×2000.

by him to be the pycnidial stage of *Hypocrella raciborskii* sensu Petch. *A. aleyrodis* is rarely found in association with a perithecial stage which appears to be *Hypocrella libera*. The perithecial stages of the two species of Hypocrella are also very similar and it is doubtful that they should be maintained as distinct species.

ASCHERSONIA GOLDIANA Sacc. & Ellis, Syll. Fungorum **14:** 990. 1899.

This species was described from a collection on white fly on Vitex collected by E. A. Goldi in Para, Brazil, communicated by T. D. A. Cockerell under the name *Aschersonia pulcherrima*. The type occurs under *Aschersonia pulcherrima* in the Ellis collection No. 7095 of the New York Botanic Garden and parts of the type collection also occur in the Farlow Herbarium No. 3984, and in Mycological Collections at Washington under *Aschersonia goldiana*.

The stromata (fig. 8) are scutate, 2–4 mm wide, white or yellowish with broad thin membranous hypothalli. The stromata are crowded and coalesce to form extensive crusts. The orifices of the pycnidia are wide and scattered. The stromata are covered with brownish copious masses of pycnidial exhudate (fig. 8). The pycnidia are ovoid with wide mouths. The pycnidiospores are fusoid, $12–16 \times 1.5–2\ \mu$ with acute ends and the paraphyses filiform up to $175\ \mu$ long.

This is the species which has been erroneously reported from Florida as *Aschersonia flavocitrina* which has discoid yellow stromata and larger pycnidiospores (see fig. 12). *A. goldiana* differs from *A. aleyrodis* only in the color of the pycnidial exhudate which when fresh is orange for *A. aleyrodis* and yellow for *A. goldiana*. On account of the color changes in dried specimens it is not possible to distinguish the species in herbaria with any accuracy. It is doubtful that they should be maintained as more than varieties.

ASCHERSONIA CAESPITICIA Syd. Englers Bot. Jahrb. **54:** 260. 1916.

This species was described from a collection of C. Ledermann No. 6856 from Hauptlager Malu, New Guinea. The type in the herbarium of the Naturhistoriska Riksmuseet of Sweden has been studied. The stromata (fig. 9) are pulvinate to hemisperhical, 1–3 mm wide, light brown and densely tuberculate. The tubercules are ellipsoid to cylindric and are sterile. The pycnidia occur in the base of the stromata and are irregularly labrinth-form. The pycnidiospores are fusoid $8–10 \times 1.5\ \mu$ with acute ends. Paraphyses were not found.

Petch (1921) has concluded that this is the pycnidial stage of *Hypocrella amomi* Rac. which produces perithecia in tubercles.

ASCHERSONIA BASICYSTIS Berk & Curtis. Jour. Linn. Soc. **10:** 352. 1869.

This species was published as No. 558 of Fungi Cubenses and was based on a collection from Cuba by C. Wright, No. 766. Three specimens bearing this number are in the Farlow Herbarium. The stromata (fig. 10) are somewhat capitate narrowing below the head and expanding over the substratum into a wide membraneous hypothallus. This is a form for which Petch has used the term studshaped. The heads are 1.5–2 mm wide, yellowish and smooth. The hyphae of the interior are

irregularly loosely interwoven. There is an outer modified cortical layer, 100 μ or more thick, consisting of narrower hyphae which are closely interwoven at right angles to the surface. The pycnidia occur in the narrow neck and are ovoid to irregular sometimes coalescing, 500–550×200–350 μ. The pycnidiospores (fig. 11) are fusoid 10–12×2 μ having cells 4–8×2 μ with the wall at the end attenuately thickened 2–3 μ. Paraphyses do not occur.

This is the pycnidial stage of *Hypocrella phyllogena* Mont. for which Montagne (1840) described similar studshaped stromata. The perithecia when formed are produced in the head. The pronounced attenuately thickened walls at the ends of the pycnidiospores separate this species from most other species of Aschersonia.

ASCHERSONIA PITTIERI P. Henn. Hedwigia **41:** (104). 1902.

This species was described from a collection by H. Pittier on *Citrus aurantium* from Cocos Island, Costa Rica. A specimen in the herbarium of the Naturhistorska Riksmuseet of Sweden is probably a part of the type. The stromata are poorly developed, hemispherical to irregular with disk-like projections, white and pruinose. The pycnidia are ovoid, 150–250×100–150 μ, several occuring in a disk. The pycnidiospores are broadly fusoid, 10–12×3–4 μ with acute ends. As Petch (1921) has concluded this is *Aschersonia turbinata*.

ASCHERSONIA VIRIDANS (Berk. & Curtis) Pat. Bul. Soc. Myc. France **7:** 48. 1891. *Hypocrea viridans* Berk. & Curtis, Jour. Linn. Soc. **10:** 376. 1869.

This species was described as *Hypocrea viridans* from a collection by C. Wright No. 450 from Cuba, on leaves of Gesneria (Fungi Cubenses No. 756). Parts of the type specimen occur in the Curtis collection of the Farlow Herbarium and in the general herbarium. The stromata are discoid to flattened pulvinate 1–1.5 mm wide, olivaceous, having a slight or no hypothallus. The pycnidia are globoid, 300–400 μ, with short ostioles. The orifices of the pycnidia are peripheral or scattered and medium in size. The pycnidiospores are fusoid, 12–16×2 μ with acute ends. The paraphyses are, filiform up to 100 μ long. Perithecia do not occur in the type.

Petch (1921) has described perithecia and placed the species in Hypocrella as *H. viridans* from collections by Thaxter from Trinidad. Although it is a fairly common species in the American tropics it apparently rarely produces perithecia.

ASCHERSONIA VIRIDULA Sacc. Ann. Myc. **11:** 547. 1913.

This species was described from a collection by S. Bonansea on Malvaviscus from Vera Cruz, Mexico. There are two specimens in the Farlow Herbarium 4026, 4027 which are parts of the type collection. The stromata are discoid, 1–1.5 mm wide, green, punctate from ostioles of the pycnidia and have slight hypothalli. The pycnidia are globoid, 350–400 μ wide. The pycnidiospores are fusoid, 12–14×2 μ, with acute ends and the paraphyses filiform up to 200 μ long. As concluded by Petch (1921) this is *Aschersonia viridans*.

ASCHERSONIA DISCIFORMIS Pat. Bul. Soc. Myc. France **8:** 136. 1892.

This species was described from a specimen collected on leaves of Cestrum by G. de Lagerheim at Puente de Chimbo, Ecuador. The type is in the Patouillard collection of the Farlow Herbarium and a portion of the type is in the general herbarium. The stromata are discoid, 1–2 mm wide, circular to slightly crenulate, olivaceous or green. The orifices of the pycnidia are large and arranged in a peripheral circle. A slight hypothallus occurs. The pycnidia are globoid, 300–500 μ in diameter, with short wide ostioles. The pycnidiospores are fusoid $12\text{–}18 \times 2\ \mu$ with acute ends and the paraphyses are filiform, 75–125 μ long. White stromata of *Aschersonia basicystis* occur with those of *A. disciformis.* As Petch (1921) has concluded this is *A. viridans.*

ASCHERSONIA BADIA Pat. Jour. Botanique **11:** 370. 1897.

This species was described by Patouillard from a specimen collected by P. Bon No. 5053, Ngoc Au, Tonkin. The type is in the Patouillard collection of the Farlow Herbarium and a portion is also in the general collection of the Farlow Herbarium No. 3960. The stromata (fig. 15) are discoid, 1–2 mm, circular to somewhat crenulate, light to dark brown with slight or no hypothallus. The orifices of the pycnidia are scattered, small and punctate. The pycnidia are subgloboid, 250–300 μ wide, with narrow short ostioles. The pycnidiospores are fuosid, $10\text{–}14 \times 2\text{–}2.5\ \mu$ with acute ends and the paraphyses are filiform up to 80 μ long. This species differs from *A. viridans* mostly in color.

ASCHERSONIA CRENULATA Pat. Jour. Botanique **14:** 244. 1900.

This species was described from collections made by M. A. Chevalier on Lonchocarpus and Smilax from Bignona, Fogny, Casamance, French West Africa. The specimens are in the Patouillard Collection of the Farlow Herbarium. The stromata (fig. 14) are discoid, 1–4 mm wide, crenulate, light brown, and surrounded by a slight hypothallus. The orifices of the pycnidia are scattered, small and punctate. The pycnidia are flask-shaped, $300\text{–}450 \times 200\text{–}250\ \mu$. The pycnidiospores are fusoid, $12\text{–}14 \times 2\ \mu$ with acute ends and the paraphyses are filiform up to 200 μ long. This species is very similar to *A. badia* except for the larger, lighter brown, crenulate stromata and the somewhat longer paraphyses.

ASCHERSONIA FLAVO-CITRINA P. Henn. Hedwigia **41:** 307. 1902.

This species was described by Hennings from a collection of Puttemans, No. 362, on leaves of Psidium from São Paulo, Brazil. The type in the herbarium of the Naturhistoriska Riksmuseet of Sweden has been studied. The stromata (fig. 12) are discoid, 2.5 mm wide, lemon-yellow with a broad hypothallus. The orifices of the pycnidia are moderately large and are arranged in a peripheral circle. The pycnidia are flask-shaped, $500\text{–}650 \times 300\text{–}350\ \mu$. The pycnidiospores are fusoid, $14\text{–}20 \times 2\ \mu$ and the paraphyses are filiform up to 125 μ long.

Hennings noted the similarity to *Aschersonia blumenaviens* P. Henn. which was also described by him (1902) earlier in the same volume of Hedwigia from a collection from Brazil. Petch (1921) has concluded that they are the same species. Hennings however states that *A. blumenaviens* is distinguished by the lack of paraphyses. The type of

the later has not been seen and probably does not exist, but on the basis of Hennings statement *A. flavo-citrina* is not conspecific.

ASCHERSONIA INTERMEDIA Petch, Ann. Roy. Bot. Gard. Peradeniya **7:** 325. 1922.

This species was described from collections on an aleyrodid made by R. Thaxter at Corral, Chile. There are 7 collections in the Farlow Herbarium Nos. 3986, 3987, 3988, 3989, 3990, 3991, and 5341 collected by Thaxter in December 1905 and January 1909 at Corral, Chile and determined by Petch as *A. intermedia.* Number 3991 is designated "cotype". The stromata (fig. 16) are discoid, ringshaped with depressed sterile centers or horseshoe-shaped. They are small 0.5–1.5 mm wide or rarely 2 mm, waxy, light yellowish brown or sometimes darker and have a narrow hypothallus. The orifices of the pycnidia are small usually in a peripheral circle. The pycnidia are globoid, ovoid or irregular. The pycnidiospores (fig. 17) are oblong or allantoid, $4–7 \times 1–1.5\ \mu$ with rounded ends and the paraphyses are filiform, $50–150\ \mu$ long.

The ring- and horseshoe-shaped stromata apparently are caused by their development only on the margins of the insect. The pycnidiospores are unusually small.

ASCHERSONIA LECANIOIDES P. Henn. Hedwigia **41:** 145. 1902.

This species was described from a collection made by Zimmerman at Buitenzorg, Java. There is a collection No. 3992 in the Farlow Herbarium which probably is a part of the type. It has yellowish, scutate to pulvinate stromata, 3–4 mm broad with wide hypothalli. The orifices of the pycnidia are scattered and medium in size. The pycnidiospores are fusoid, $12–16 \times 2\ \mu$ with acute ends. This is *Aschersonia placenta* as concluded by Petch (1921).

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Mutations of the Self-Incompatibility Gene (S) and Pseudo-Compatibility in Angiosperms[+]

Kamla Kant Pandey*

(*Department of Botany and Plant Pathology, The Ohio State University, Columbus 10, Ohio*)

I. THE SELF-INCOMPATIBILITY GENE

Recent studies of the mutations of the self-incompatibility gene in *Oenothera*, *Prunus*, and *Trifolium* spp. (Lewis, 1951; Lewis and Crowe, 1954; Pandey, 1956*a*; Crowe, 1955) have shown that there are at least three components of the **S** gene in these species: the male component which governs the reaction of the pollen grain, the female component which governs the reaction of the style, and the pollen growth component which governs the production of substance or substances necessary for pollen germination and pollen tube growth. Four kinds of mutations of the **S** gene have been identified: (1) "Revertible" mutations which are temporary and revert to their normal reaction before the seed develops or during seed development. The reverted mutant seedling is, therefore, normal and self-incompatible. These mutations differ from "reversible" mutations in that the revertible mutation is believed to be due to the unstable state of the gene which after a few cell divisions either gives a permanently mutated gene or reverts to the normal original state, there is no reversion from a stable mutated gene to the original state as is the case in "reversible" mutations. (2) Pollen reaction mutation. (3) Style reaction mutation. (4) Both pollen and style reaction mutations.

The degree of self- or cross-fertility achieved by spontaneous or X-ray induced mutations varies greatly from very low to full fertility. It suggests that there may be a number of genic elements in each of the male and female parts of the **S** gene. Generally, the level of self-fertility in the progeny of such mutant plants is lower than that of their parents. The lower fertility in the second generation of these plants does not seem to be entirely due to inbreeding depression because these plants, though slightly less vigorous than their parents, have normal pollen fertility, and produce full seed set in compatible crosses (Pandey, 1956*a*). Murphy (1942) in *Agropyron cristatum* and Myers (1948) in *Dactylis glomerata* also found that self-fertility in the progeny of a naturally occurring pseudo-fertile plant decreases considerably and that "the decrease could not be wholly explained by the inbreeding effect". Myers concluded that reduced vigor among inbred progenies was not of major importance in conditioning a reduction in self-fertility but that the reduced seed set accompanying inbreeding was associated with a decrease in true self-compatibility resulting from inbreeding. It has been suggested that this decrease in pseudo-self-compatibility is due to the small amount of available metabolite, in the pollen grain of

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[+]Publication number 607, Department of Botany and Plant Pathology.

*Present address: Dr. John Innes Horticultural Institution, Bayfordbury, Hertford, Herts. England.

the inbred progeny, a condition which allows a faster conversion of incompatibility precursors into incompatibility substances (Pandey, 1960).

In the normal diploid self-incompatible species the minor genes which, if expressed, may disturb self-sterility, have accumulated under the cover of the strong incompatibility reaction of the major **S** alleles. Assuming these minor genes are located on different chromosomes and that there are no groups of these genes which are linked with other genes which may be responsible for characters of evolutionary or economic significance, the distribution of such minor genes in the population, due to the absence of selection pressure, should be random and even. Under such circumstances, the percentage of seed set in genetically pseudo-self-fertile plants may be expected to indicate, reasonably, the degree of mutation of the **S** gene, provided the plants concerned are at the same state of inbreeding. However, mutations causing a very small change of reaction will not be reflected in seed production. Only after a minimum degree of mutation, in which the self-incompatibility reaction is sufficiently weakened, are the minor genes able to influence the growth of pollen tubes and produce some seed. The detection of the degree of mutation by the present criterion would only be possible when the degree of mutation is beyond this minimum threshold. However, a very low number of selfed seeds from a plant may not be due to a partially mutated **S** allele contained by it but may be due to the current mutations occurring in its normal **S** alleles.

II. TYPES OF PSEUDO-COMPATIBILITY

Pseudo-compatibility can be classified into 3 groups:

1. *Environmental pseudo-compatibility.*—This is caused by the external (temperature, day length etc.) and internal (age and vigor) environments of the plant. *Solanum rybinii* (Pushkarnath, 1953) and *Physalis ixocarpa* (Pandey, unpub.) are fully self-incompatible during summer but are partially self-compatible in cooler autumn or winter conditions. In *Brassica* species, cyclic mid-season and end-of-season pseudo-compatibility has been reported (Stout, 1938). It has been suggested that the available metabolite content in the pollen and style affects the conversion of incompatibility precursors into incompatibility substances. A high concentration of metabolites is toxic to the presumably enzymatic conversion reaction (Pandey, 1960). The tendency in plants to store energy giving substances in the reproductive organs during the late growing and flowering seasons may, therefore in certain plants bring about a decreased production of incompatibility substances and pseudo-compatibility. Plants showing environmental pseudo-compatibility, however, are fully self-incompatible when they are of proper age and vigor and are grown under suitable environmental conditions.

2. *Artificial pseudo-compatibility.*—This is brought about by mechanical, chemical or environmental treatment of plants or flowers: (i) Bud pollination—Pseudo-compatibility has been obtained in a number of species by pollinating flowers with mature pollen in the bud condition, when the style is immature and presumably has not yet

developed the full strength of incompatibility substance (Sears, 1937; Stout, 1938). In *Forsythia intermedia* this has been achieved by pollinating mature styles with immature pollen (Moewus, 1950). (ii) Chemical treatments: Boric acid has been found to stimulate pollen germination and pollen tube growth in several species (Schmucker, 1934). Its efficacy in the negation of self-incompatibility has been shown by Moewus (1950) and has been thought to be due to the formation of inactive complexes of boric acid with the inhibitory substances. It has been claimed that treatment of flowers with α-naphthalene acetamide (Eyster, 1941) may bring about pseudo-fertility. The hormone treatment of flowers has been found to delay the formation of abscission layer thereby giving more time to the slow growing pollen tubes to grow down and achieve fertilization (Lewis, 1946). In plants with a weak self-incompatibility reaction this treatment may thus bring about self-fertility. Emsweller and Stuart (1948) obtained a substantial number of seeds after incompatible pollinations in *Lilium* by treating the ovaries with growth regulating substances. However, it is not known whether this is due to the longer life of the style, to a real primary effect on the incompatibility reaction, or to some other cause. (iii) Mechanical manipulation: In certain species the removal of the stigmatic secretion by washing resulted in self-fertilization (Yasuda, 1928). Shaving or wounding of the stigma and amputation or grafting of styles, thus removing the part of the style containing the incompatibility substances, have in certain species made the production of selfed seeds possible (Brink, 1934; Sears, 1937; Oelke, 1957).

3. *Genetic pseudo-compatibility.*—This may be caused by the following factors: (i) Chance combination of modifier genes which weaken the incompatibility reaction (*Petunia*—Mather, 1943; *Nicotiana*—East, 1934). In *Antirrhinum majus* (Tseng, 1938) and *Nictiana* spp. (Brieger, 1930) self-fertility in certain cases has been attributed to another gene which is epistatic over the **S** alleles. (ii) By natural or artificially induced mutations of the incompatibility alleles (*Oenothera organensis-Prunus avium* and *Trifolium* spp.) (iii) By the inappropriate combination of **S** alleles with respect to the dominance relationship in the

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EXPLANATION OF FIGURES

FIG. 1. Crossing over separating the two parts of the **S** gene giving composite alleles, $\mathbf{S}^{2♂}_{4♀}$ and $\mathbf{S}^{4♂}_{2♀}$.

FIG. 2. Crossing over separating the genic elements of the ♂ part of the **S** gene giving composite alleles, $\mathbf{S}^{2♂.4♂}_{4♀}$ and $\mathbf{S}^{4♂.2♂}_{2♀}$.

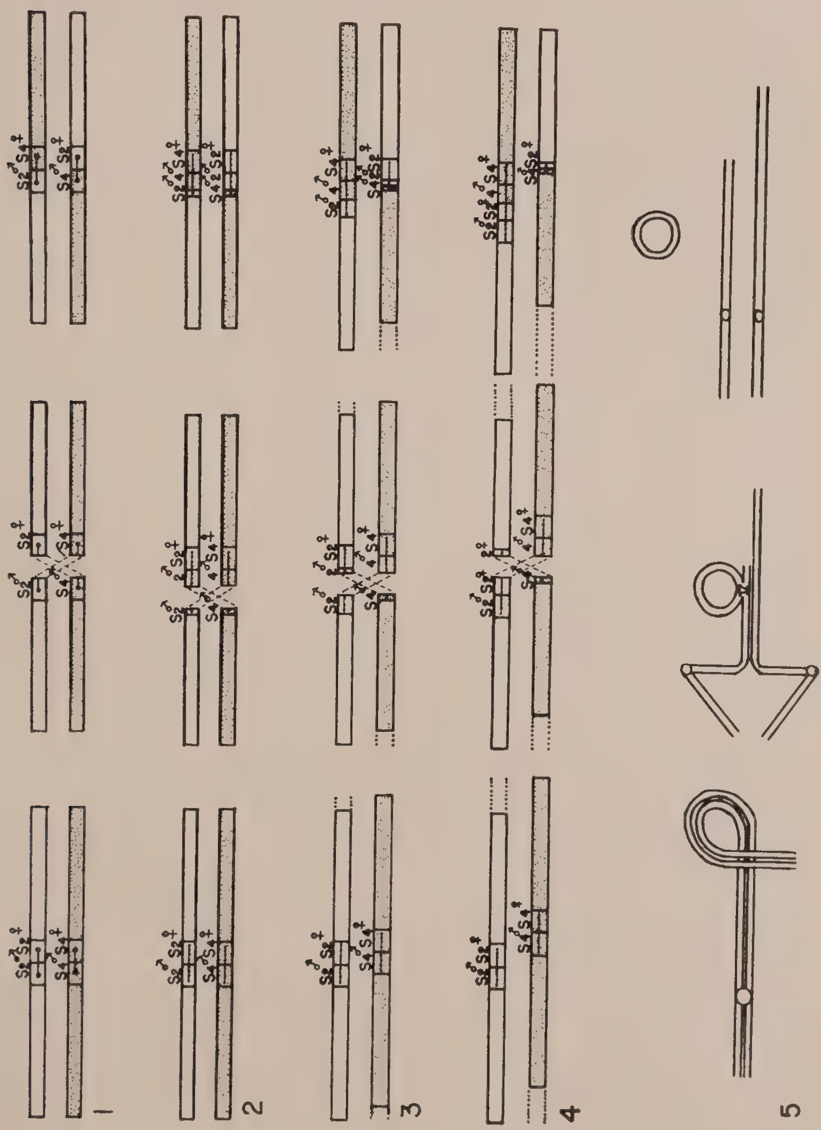
FIG. 3. Synaptic equivalance leading to unequal crossing over giving composite alleles, $\mathbf{S}^{2♂.4♂}_{4♀}$ and $\mathbf{S}^{4♂.2♂}_{2♀}$

FIG. 4. Synaptic equivalence leading to "extreme-end-pairing" giving composite alleles, $\mathbf{S}^{2♂.4♂}_{2♀.4♀}$ and $\mathbf{S}^{4♂}$

FIG. 5. Intra-chromatid association at prophase leading to sub-chromatid breaks and deletion.

pollen and style. The last example (iii) is possible only in species with a sporophytic system of incompatibility (Pandey, 1956*a*) or in those species with a gametophytic system having two series of **S** alleles (Pandey, 1957).

Besides the major genes there are also minor (weaker) genes which affect self-incompatibility. This has been clearly demonstrated in the incompatibility reaction in the autotetraploids of *Trifolium pratense*



(Pandey, 1956*b*). In this species, unlike the diploids, different individuals of the same genotype in tetraploids have different selfed pollen tube growth, different selfed seed set, and different reactions of their pollen tube to temperature. It has been proposed that the major weakening of incompatibility by allelic competition allows minor genes, which have no obvious effects in the diploids, to manifest themselves.

When pseudo-self-compatibility is controlled by a stable mutated **S** allele all the selfed progeny will be self-compatible like their parent, when it is controlled by an unstable **S** allele self-incompatible as well as self-compatible plants will occur in the selfed progeny. The degree of pseudo-compatibility caused by unstable **S** alleles would depend on the mutation rate which is intrinsic to the particular allele concerned (Pandey, 1956*a*). Furthermore, one allele can have an effect on the mutation rate of the other accompanying allele (Lewis, 1951).

One of the simplest methods to distinguish pseudo-compatibility due to mutation in **S** alleles from that due to environmental or other genetical reasons would be to ascertain the proportion of different genotypes in the progeny. Environmental and polygenic effects would usually weaken the self-incompatibility in general and thus would yield two homozygous and one heterozygous genotypes in the proportion of 1Sa.a: 2Sa.b: 1Sb.b. All plants obtained due to environmental pseudo-compatibility would be self-incompatible when grown under suitable environmental conditions. Plants obtained by mutations in the **S** alleles may be only of 2 genotypes, since often only one of the 2 alleles is mutated or is unstable. If, however, all the 3 genotypes are recovered in the progeny, their proportions would generally be quite different from those expected on the basis of environmental or other genetical effects. Moreover, some or most of the plants resulting from mutation may contain permanent mutations giving various degrees of pseudo-compatibility.

Discussing the origin and behavior of self-fertile plants in otherwise self-incompatible species, Pandey (1956*a*) concluded that in the gametophytic species pseudo-compatibility in nature generally arose from mutations in the **S** alleles. On the basis of the difference between gametophytic and sporophytic species, in behaviour of the selfed progeny of pseudo-compatible plants he suggested that pseudo-fertility in sporophytic species in certain cases may be due to different dominance relationships between the **S** alleles in the pollen and style. However, the most common cause of the widely naturally occurring phenomenon of pseudo-compatibility in the homomorphic sporophytic species is believed to lie in environmental effects on the sensitive mechanism of the **S** allele expression in this type of incompatibility system (Pandey, 1958). Thus the origin of natural pseudo-compatibility in homomorphic species is mostly mutational in the gametophytic species and non-mutational (environmental) in the sporophytic species. Furthermore, mutations that affect the **S** alleles only slightly and are undetectable in the gametophytic system may have exaggerated effects in producing seed in the sporophytic system due to its being sensitive to environmental effects. Artificial pseudo-compatibility may be obtained in either gametophytic or sporophytic species without any relationship to the incompatibility systems.

III. PSEUDO-COMPATIBILITY DUE TO MUTATIONS IN THE S GENE

In the light of the knowledge gained of the nature of the incompatibility gene through the study of spontaneous and X-ray induced mutations, the earlier concept of the pseudo-compatibility gene requires re-examination. Reports in the literature of self-fertility, unrelated to the age of flower, age of the plant, or seasonal conditions, in otherwise highly self-incompatible species are not uncommon and have been reviewed by Stout (1938). In six species, *Nicotiana langsdorffii* (East, 1929); *Trifolium pratense* (Williams and Silow, 1933); *Antirrhinum glutinosum* (Gruber, 1932), *Beta vulgaris* (Owen, 1942), *Papaver nudicaule* (Fabergé, 1942) and *Trifolium repens* (Atwood, 1945), the self-fertility has been ascribed to S_f alleles of the **S** series. The S_f alleles are believed to have arisen as mutations of the **S** alleles.

Among the species which show natural pseudo-compatibility due to changes in the reaction of the **S** alleles, only in *Trifolium hybridum* (Williams, 1951) has the nature of these changes been studied in some detail. Williams suggested that the S_a and S_c alleles in the selfed progeny of the pseudo-self-compatible plants $S_{a.b}$ (family La/77) and $S_{c.d}$ (family La/87) respectively, behaved as very strong inhibitors of pollen tubes when present in the homozygous condition ($S_{a.a}$ and $S_{c.c}$), but were rendered considerably less efficient when present in the heterozygous condition such as in the styles of $S_{a.b}$ and $S_{c.d}$. However, a re-examination of Williams' data shows that (1) there is an absence of one of the homozygous groups in the progeny in both the selfed families there occurring only 2 ($S_{a.b}$—$S_{a.a}$ and $S_{a.b}$; $S_{c.d}$—$S_{c.c}$ and $S_{c.d}$) instead of 3 groups. And (2) the above explanation fits only when 1 plant in the family La/87 is ignored. This plant, although homozygous $S_{c.c}$, has an even higher pseudo-compatibility than the heterozygotes. This is entirely contrary to the above hypothesis. No satisfactory explanation of this plant has been given.

An alternative explanation involving mutations of **S** alleles fits the data better. If it is assumed that in the parent plant ($S_{c.d}$) of the family La/87 the allele **S**c was unstable and produced mutations, the progeny would give only 2 groups, $S_{c.c}$ and $S_{c.d}$ in the ratio of 1:1. The number of plants, though low (4 in each group), is entirely in agreement with the expectation. On this assumption, the absence of one of the homozygous groups as well as the occurrence of equal numbers of plants in the homozygous and heterozygous groups is explained. The same explanation, assuming that the **S**a allele in the parent plant $S_{a.b}$ was unstable, seems also to be applicable for the similar behaviour of the family La/77 (5 plants in each of the 2 groups).

In the homozygous groups $S_{c.c}$ of the family La/87, the female part mutation in one of the **S**c alleles (designated as $S_{c}{\female}_{c}$) will not be expressed since the other allele covers its effect (Pandey, 1956*a*). Thus, in $S_{c.c}$ plants mutation in one of the alleles can only be effective in producing seed if it takes place in the male part. However, in a plant which has female part mutations in both **S**c alleles ($S_{c.c}^{\female\,\female}$) mutation will be expressed. But such plants must occur by chance combination of male and female gametes, both of which contain female part mutations in the **S**c allele, and must be very rare. From the behaviour of

the exceptional plant in family La/87 in various crosses it is evident that in addition to having a high degree of male mutation this plant is also homozygous for the female part mutation in its Sc alleles. It is, therefore, highly pseudo-self-compatible in spite of its being homozygous for the Sc allele.

The much higher pseudo-compatibility in the heterozygous $S_{c.d}$ plants is due to the fact that here both female and male part mutations are expressed. Thus the significant difference in the pseudo-compatibility exhibited by the 2 incompatibility groups ($S_{c.c}$ and $S_{c.d}$) may be due to the difference in the expressions of the male and female part mutations in the homozygous and heterozygous plants and not due to the weakening action of the allele Sc in the heterozygous state ($S_{c.d}$) as is postulated by Williams.

IV. NATURE OF THE S GENE MUTATIONS

1. *Conventional crossing-over.*—Critical tests have proved that the pollen and stylar parts of the **S** gene are specific in reaction (Lewis, 1949). If a cross-over occurs which separates the 2 parts of the normal alleles, *e.g.* $S_{2♀}{}^{2♂}$ and $S_{4♀}{}^{4♂}$ of a plant of the constitution **S**2.4, the situation is identical with pseudo-allelism and can give rise to pollen of the constitution $S_{2♀}{}^{4♂}$ and $S_{4♀}{}^{2♂}$. A plant producing some pollen with such composite alleles, barring position effect, will remain completely self-incompatible (Pl. 1, Fig. 1). Only if a plant of different **S** constitution ($S_{1.3}$) is pollinated by pollen containing the composite allele ($S_{4♀}{}^{2♂}$) will the resulting seedling be self-compatible. Lewis (1949) did not find any such composite allele among the several plants tested. However, the possibility of the formation of this type of composite allele cannot be ruled out.

It has been suggested earlier that there may be a number of genetic elements in each segment (part) of the **S** gene. If there is crossing-over between the different elements of the ♂ segments of the 2 different alleles, pollen may be formed which may contain some male elements from both the alleles (Pl. 1, Fig. 2). From studies of autotetraploids, it is known that certain alleles, when present together in pollen, weaken the incompatibility reaction of the pollen because of competition interaction between the male parts of the 2 alleles (Lewis, 1947). This may bring about partial or full self-compatibility. It may be assumed that a pollen grain in which the male part of the **S** allele is composed of male elements from 2 different **S** alleles could exhibit competition interaction. With this hypothesis, however, mutation in one allele of a plant should generally be accompanied by mutation in the other allele also. Such reciprocal recombination products have not been found. Mutations of the ♂ part of the same allele, leaving the other allele unchanged, have been consistently found in a number of plants studied in *Oenothera*. This would appear to be similar to the phenomenon of gene conversion observed in *Neurospora*, *Aspergillus* and *Drosophila* (Lawrence and Bonner, 1957). However, the **S** gene mutation, which involves a composite nature of the elements in its ♂ part, will bring about self-fertility only if the 2 components of the ♂ part show competition interaction. In *Oenothera* ♂ part mutations have been found in plants in which the **S** alleles did

not show competition interaction when tested in the autotetraploid condition (Lewis, 1947; 1951).

The mutations in *Oenothera* could, however, be explained if it is assumed that the recombination between the male elements from 2 different **S** alleles produces a new pollen specificity which would make this composite pollen compatible on its parent style. Such recombination products between the elements of **S** alleles producing new specificity have been found in lower plants, *Schizophyllum commune* (Kniep, 1930; Papazian, 1951) and *Coprinus lagopus* (Day, 1959).

2. *Unequal crossing-over.*—There is another method by which crossing-over in a compound gene may result in mutation. Stadler's work (1954) on maize suggested that there is a "synaptic equivalence" in the genic elements at the **R** locus which leads to unequal crossing-over between the genetic elements of this gene. In the compound, self-incompatibility gene synaptic equivalence would produce crossing-over which would lead to deficiency in one allele and duplication in the other (Pl. 1, Fig. 3). A pollen grain containing a deficiency of the pollen part will be compatible on its parent style. Pollen grains containing the corresponding duplication of the genic elements may or may not be compatible according to the presence or absence of competition interaction. The occurrence of mutations in *Oenothera*, in which competition interactions of **S** alleles are weak and ineffective in producing selfed seed, would be explained on this basis. The failure to recover reciprocal recombination product thus producing mutations of only one **S** allele may be due to the loss of the pollen growth part of the **S** allele in one of the recombination products. Pollen grains with such a recombinant **S** allele will be inviable (Figs. 3 and 4).

With irradiation the frequency of the complete mutations, including both ♂ and ♀ parts, is generally increased (Pandey, 1956*a*). This would be possible on the assumption that irradiation in some way increases the magnitude of the unequal synapsis ("extreme-end-pairing", Pl. 1, Fig. 4) resulting in large deficiencies of both segments. This type of deficiency may only rarely occur in nature. According to this hypothesis mutations could occur only during meiosis and would not take place in somatic tissue. However, Lewis (1948), in his studies with spontaneous mutations in *Oenothera*, traced many of his mutations to the sporogenous cells.

3. *Sub-chromatid breakage.*—The experiments of La Cour and Rutishauser (1953) on the irradiation-induced chromosome breakage in *Scilla sibirica* endosperm indicated that sub-chromatid breaks during mitotic prophase could result in deficiencies. These deficiencies are due to the sub-chromatid breakage and reunion in coiled and overlapping chromatids at prophase. The intrachromatid associations form loops which may be deleted (Pl. 1, Fig. 5). A causal relationship between sub-chromatid breakage and delayed mutation has been pointed out by Lewis and Crowe (1953) in the study of mutations of **S** alleles. They obtained a revertible mutation in *Prunus* species with irradiation of prophase; only stable, complete mutations occurred with treatment of the resting stage. The cytological basis for this has been provided by Darlington (1950), who suggested that the revertible mutation is due to the sorting out of mutated from unmutated poly-

peptide chains composing the chromosomes. Accordingly, sub-chromatid breakage may involve only a few strands (polypeptide chains) of a chromatid leaving others intact. The partially deficient chromosome in further mitotic divisions would give rise to chromosomes some of which may be completely deficient for a particular region (giving permanent mutations) while others may be fully restored normal chromsomes (giving revertible mutations). Thus mutations of the **S** allele traced to the premeiotic cells may be explained on the basis of sub-chromatid breakage.

4. *"Complementary" mutations.*—Stadler (1954) found that not all mutants of **R** in maize were accompanied by crossing-over. It was necessary to assume that both **S** and **P** (2 parts of the **R** gene) were capable of mutating to the so-called "null" forms **p** and **s** in a conventional gene mutation manner *i.e.* without crossing-over. In *Drosophila* the Bar gene, besides producing normal and Bar-double mutations through unequal crossing-over, also gives rise to true mutations (Infra-Bar) which have no relation to unequal crossing-over in their mode of origin. Likewise, there is a possibility of genuine "constructive" mutations occurring at the **S** locus in addition to the mutations produced by crossing-over, sub-chromatid breakage or other such means.

Many mutations of **S** alleles could be equally explicable by mutations of a qualitative nature not arising from crossing-over as well as by loss mutations. The functionally specific and interdependent nature of the ♂ and ♀ parts, of the **S** gene would imply that loss changes and qualitative changes would lead to a similar result—creating disharmony in the 2 parts of the **S** gene. This would result in the breakdown of self-incompatibility. Thus, the pollen-controlling part of the **S** gene may mutate to a new type of incompatibility reaction, the style-controlling part remaining unchanged—"independent" mutation. In this case self-pollination will be compatible, not because the pollen fails to develop any reaction, but because it develops a reaction which is not corresponding to that in the style. For the creation of a new **S** allele in one step, therefore, mutations in both parts of the **S** gene will have (1) to occur simultaneously and (2) to be in a harmonious direction *i.e.* "complementary" in nature. This would be very rare under any circumstances.

Assuming complementary mutations do occur and that they take place in several steps changing the specificity only slightly each time, it may be possible to obtain such mutations from the naturally occurring mutations which are of small magnitude, but not from the irradiation-induced mutations which are liable to be of extreme magnitude and would probably be loss changes. There are some indications of this type of mutation from the *Trifolium hybridum* data discussed above but since the effects of deleterious genes, polygenes or zygotic lethality cannot be ruled out as alternative explanations, this interpretation is only conjectural.

It is well known that the number of possible ways in which a gene can mutate is limited largely by the nature of the gene itself. Some genes, for instance those controlling flower color, can mutate to a number of new states (alleles). Yet the possibilities are not unlimited since

the directions which the effects of mutations can take are also conditioned by the developmental and physiological system resulting from the action of the other genes already present (Müller, 1949). While there may be innumberable kinds of qualitative (genuine) mutations in the ♂ and ♀ parts of the **S** gene, the possible "stable" states into which they could be converted may be relatively limited. Under such circumstances the evolution of a new **S** allele from an old one by gradual selection of those mutations in the ♂ and ♀ part which are "complementary" in nature may not be as rare as it may seem. Due to the small effects of such natural mutations, it would be hard to prove or disprove the validity of this assumption.

Most of the so-called "self-fertile" alleles reported in otherwise self-incompatible species are probably those **S** alleles in which the complementary nature of a part or of the full gene has been disrupted. That particular part of the allele which has thus been disrupted, would induce fertility. The immediate advantage of self-compatibility in a population will be overwhelming, provided such mutant plants and their selfed progenies are not eliminated due to serious inbreeding depression. The re-evolution of self-incompatibility in those plants, if it can occur at all, must, therefore, cover a long span of time. This would expose the plants to deviation from its original genetic system, thereby making the possibility of the re-evolution of the previous type of **S** gene system further remote. A case of secondary evolution of outbreeding from an inbreeding ancestor, which was previously self-incompatible, has been envisaged by Bateman (1955) in *Lepidium sisymbrioides*. This species has dioecious flowers, a rare occurrence in the family Cruciferae. The development of a heteromorphic type of incompatibility, dioecism and possibly monoecism would be possible as a result of secondary evolution promoting outbreeding and heterozygosity.

V. EVOLUTION OF THE S GENE AND ITS ALLELIC SERIES

In the fungi, *Schizophyllum commune* and *Coprinus lagopus* (*loc. cit.*), crossing-over between the elements of 2 different **S** alleles has produced a new functional self-incompatible allele. This is possible in the lower plants in which the 2 interacting tissues are haploids and have the same number of **S** alleles. In the higher plants the interaction occurs between the haploid male gametophytic tissue having one **S** allele and the diploid sporophytic tissue having 2 different **S** alleles. In the evolution of the gametophytic system in these plants there had to be selection against allelic competition and dominance in the style, without any such selection operating in the male gametophyte. This, in the higher plants, probably led to the evolution of 2 separate mutationally independent sub-units (parts) of the **S** gene controlling the pollen and stylar reactions. Furthermore, in order to bring about the multiallelic incompatibility the pollen and stylar parts of each allele had to be specific and complementary in nature. Thus the **S** gene in the flowering plants has a much more complicated structure than in the lower plants. The creation of a new **S** allele from a pre-existing one in one step, which has been easily possible in the lower plants, would, therefore, be (as has been stated before) very rare in the higher plants. Similar arguments lead to the rejection of East's hypothesis

(1929) that **S** alleles arose as a sudden, one step mutation from a pre-existing self-fertility gene.

It is likely that the creation of the **S** gene was a slow process, building up, fraction by fraction, the different elements of the ♂ and ♀ governing parts of the **S** complex. The genetic units comprising the **S** gene could have been derived from any of the 3 processes: (1) these genetic elements were originally located at different loci and were brought together in a single tight linkage group by translocations and inversions. (2) They were the result of tandem duplications on the model of the Bar locus in *Drosophila* followed by differentiation. Or (3) they evolved by complex changes in the closely linked genetic units which were present initially and were cumulatively responsible, as a functional unit, for the earlier comparatively simple physiology of the sexual union (pollination, pollen germination, pollen tube growth in the style, and fertilization).

"Like the outbreeding population of man and cattle, a plant population, which is adapted to cross-pollination due to its flower structure and has an environment in which a more vigorous outbreeding has a selective advantage, would be serologically heterogeneous. With such raw material already available", Bateman (1952) argues, "all that would be needed to produce a primitive oppositional system of self-incompatibility is a division of labor so that the style produced antibodies to those antigens in the pollen for which the population was heterogeneous". Self-incompatibility arose by the selection of plants with corresponding antigens and antibodies which rendered them partly self-incompatible. Since the selection of complementary (correspondingly specific) ♂ and ♀ genetic units took place independently, the specificity of the individual complementary components was different. These complementary units, strengthened by the polygenic background, gave rise to incompatibility alleles everyone of which had a distinctive specificity of its own. This hypothesis would explain the occurrence of a large number of different **S** alleles in the multiallelic system of self-incompatibility. These alleles evolved with the evolution of the system itself and were not a result of mutations from one allele to another.

SUMMARY

Pseudo-compatibility has been sub-divided into 3 categories: (1) Environmental pseudo-compatibility—caused by external (temperature, day length etc.) and internal (age and vigor) environments of the plant. (2) Artificial pseudo-compatibility—caused by mechanical (*e.g.* washing, shaving, wounding or amputation of stigma; bud pollination), chemical (*e.g.* treatment with hormones) and environmental (*e.g.* growing plants in cold temperature conditions or selfing during the end of flowering season) treatment of plants or flowers. And (3) Genetics pseudo-compatibility—caused by the modifier genes (major or polygenic), or the mutated **S** alleles, or may be the result of inappropriate combination of **S** alleles with respect to the dominance relationship in the pollen and the style. The last is possible only in the sporophytic system and in the gametophytic system with 2 series of **S** alleles.

It has been suggested that, in nature, pseudo-compatibility in the homomorphic sporophytic species is largely environmental whereas

that in the gametophytic species it is largely genetic (mostly **S** allele mutations). Artificial pseudo-compatibility can be obtained in both gametophytic and sporophytic species without any relation to incompatibility systems.

The nature of mutations of the **S** allele which cause pseudo-compatibility has been discussed in detail. The available information from different species has been critically examined in relation to: (1) conventional crossing-over; (2) unequal crossing-over; (3) sub-chromatid breakage; and (4) "complementary" and "independent" mutations. It is suggested that 4 kinds of mutations may be involved: (1) loss (deletion) mutations; (2) non-loss mutations involving crossing-over between ♂ and ♀ parts of 2 different **S** alleles resulting in a composite allele of which the 2 parts are not complementary in reaction *e.g.* $\mathbf{S}^{2♂}_{2♀}$, $\mathbf{S}^{4♂}_{4♀} \rightarrow \mathbf{S}^{2♂}_{4♀}$, $\mathbf{S}^{4♂}_{2♀}$ (3) non loss mutations involving crossing-over which result in recombination between the male elements from 2 different **S** alleles producing a new pollen specificity; and (4) non-loss mutations of a constructive nature bringing about qualitative changes (genuine mutation).

Generally mutations of only one of the 2 alleles present in a plant are obtained. This has been suggested to be due to the inviability of the pollen which contains that recombination product of crossing-over between the elements of **S** alleles which is devoid of pollen growth part. Only pollen with the reciprocal recombination product, having pollen growth part of the **S** allele (here occurring in double dose), are functional.

It has been concluded that the large number of **S** alleles occurring in the multiallelic type of incompatibility system evolved *de novo* rather than from mutations of one allele into another.

ACKNOWLEDGMENT

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On Some Male Fructifications Referable to Glossopteris and the Systematic Position of the Genus

J. Sen

(*Botanical Laboratory, University College of Science, Calcutta*)

Introduction

Undoubted fructifications of *Glossopteris* have long been missing. Two recent contributions (Plumstead 1952 and Sen 1955) on female fructifications of the genus have added a great deal to our knowledge of its affinities. The timely discovery of male organs of *Glossopteris* apparently does not aid materially in establishing its systematic position (Sen 1955).

Recently a number of sacs containing typical *Pityosporites* type of pollen have been recovered from Indian Lower Gondwana coal. Since *Pityosporites* has been assumed to be the pollen of *Glossopteris* on grounds of close association in the Lower Gondwana rocks collected from different parts of the southern hemisphere and particularly India (Virkki, 1945; Ghosh and Sen, 1948; Sen, 1948), it was thought that intense search for these sporangia-like structures (referable to *Glossopteris*) might be profitably pursued. A successful find of this kind is also likely to add more definite clues to the long standing problem of the botanical affinities of *Glossopteris*.

A large number of analyses of Indian Lower Gondwana coals from Ranigunj and Karharbari stages by the present author yielded a variety of sporangia-like structures, some of which have been found associated with or containing typical pollen of *Pityosporites* type (Figs. 2–6, and 10). When smeared under a cover glass, some of them liberated numerous *Pityosporites* type of pollen grains (Fig. 6). These structures containing *Pityosporites* are as such probably related to *Glossopteris*.

Structure of the Microsporangia of Pityosporites

The microsporangia are variable (probably belonging to different species) (Figs. 2–5 and 8–11), 'sac-like structures of peculiar form' often looking like moss capsules. They occur freely and singly (possibly not otherwise obtainable in maceration), and taken as such they are unlike the sori of ferns. They appear to be sessile, somewhat elliptical, tapering at one extremity, the other end (possibly the attachment region) usually remaining relatively broad, often looking almost oval. They measure 800 μ–1400 μ x 650 μ–1000 μ.

The sporangia are unilocular, dehiscing regularly more or less in transverse plane at the apex (Figs. 2–5, 8, and 11), but apparently not so in Fig. 10; all sporangia appear exannulate. The cells of the wall are usually long, regularly and/or irregularly rectangular to rhombic (but not always so), more often their outlines are destroyed. The cell walls, when distinguishable, are predominantly sinuous but sometimes straight, especially near the base or apex of the sporangia (Figs. 3, 5, and 12–13).

The microsporangia long known to be referable to *Glossopteris are* frequently empty and exannulate bodies (Arber 1905). These so-called microsporangia occur in groups, and are probably borne on the lower concave surface of some structures transitional between scale and foliage leaves found in association with *Glossopteris browniana*. Arber compared his sporangia with those of a recent cycad, a Palaeozoic *Sphenophyllum* and the one described by Zeiller as *Discopteris Ralli*. He also referred to the earlier suspicions regarding the presence of sori like bodies found associated with *Glossopteris*.

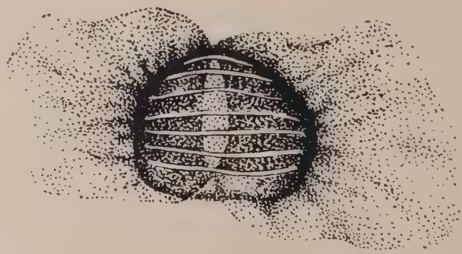


FIG. 1. *Pityosporites* sp. Characteristic pollen inside the sac as shown in Fig. 2. x 575.

In 1932 Du Toit described *Eretmonia natalensis* which might be the organ bearing the types of microsporangia already referred to by Arber (1905) and also described by Seward (1907). Du Toit interpreted his material as representing most probably the male reproductive organ of a species of *Glossopteris*.

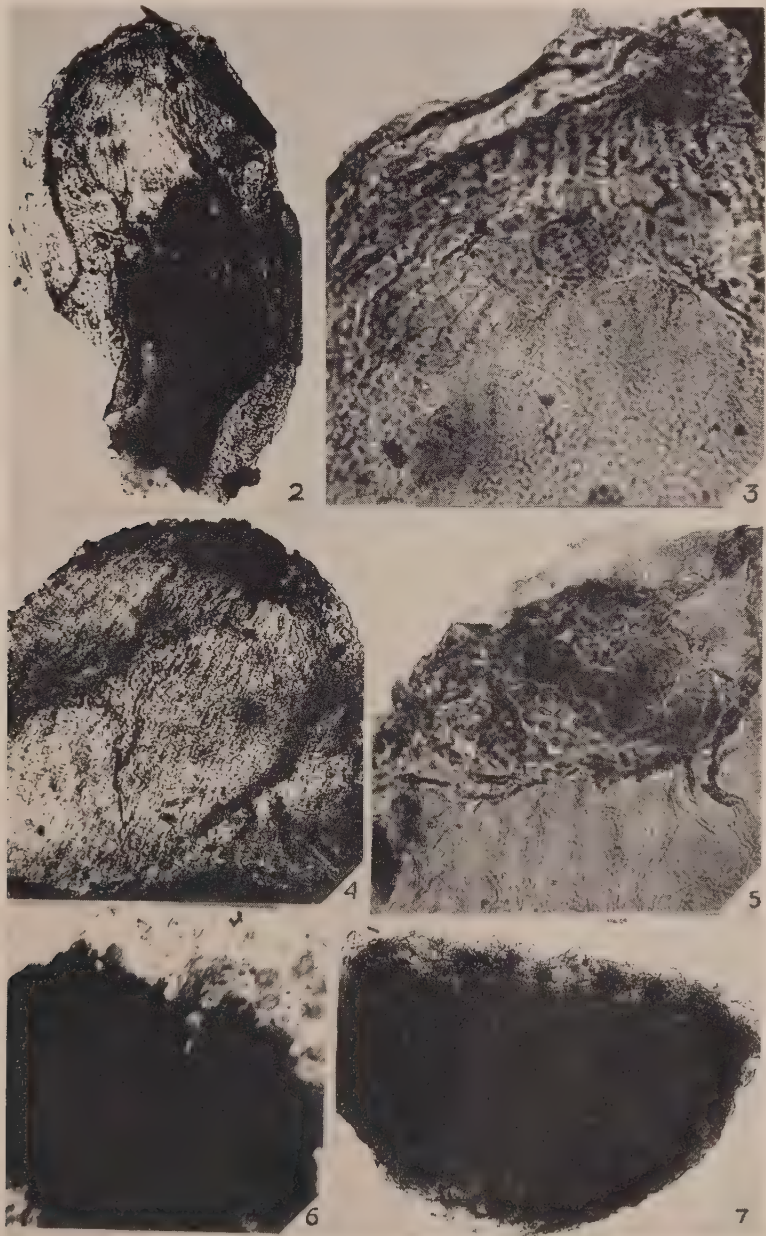
Seward and Sahni's (1920) reinterpretation of *Ottokaria bengalensis* suggested that this specimen was probably the ovulate organ belonging to a pteridosperm. But Plumstead (1952) does not altogether rule out the possibility of the species being the staminate reproductive organ of a *Glossopteris*.

In 1947 Texeira mentioned and illustrated a leaf of *Glossopteris indica* with two rows of projections, "regularly arranged, alternate, recalling the sori of certain ferns". A fragment of a leaf of *G. angusti-*

EXPLANATION OF FIGURES

FIGS. 2–7. Microsporangia containing or associated with *Pityosporites* sp. FIG. 2A. sporangium containing a few *Pityosporites* type of pollen. Note the regular nature of apical dehiscense. x 70. FIG. 3. The enlarged view of the apical portion of the figure 2. Note that the sporangium contains a few typical *Pityosporites* type of pollen. x 280. FIG. 4. A sporangium containing two *Pityosporites* type of pollen juxtaposed together (forming a black mass) near the small circular (to oval) opening. x 70. It has not been possible to get a better exposure so that the pollen and the aperture of dehiscence may be well distinguishable. FIG. 5. The enlarged view of the apical portion of the figure 4. Note the juxtaposed *Pityosporites* pollen grains near the dehisced mouth of the sporangium, and the disorganized nature of its wall cells. x 280. FIG. 6. A smeared semicarbonised sporangium showing scattered pollen of *Pityosporites* type. x 60. FIG. 7. A compact mass of *Pityosporites* type of pollen teased out of a sac-like body. x 70.

folia showing similar conditions was described earlier by Zeiller (1896). Apparently these structures are not closely comparable to the microsporangia described in this paper.



AFFINITIES OF Pityosporites

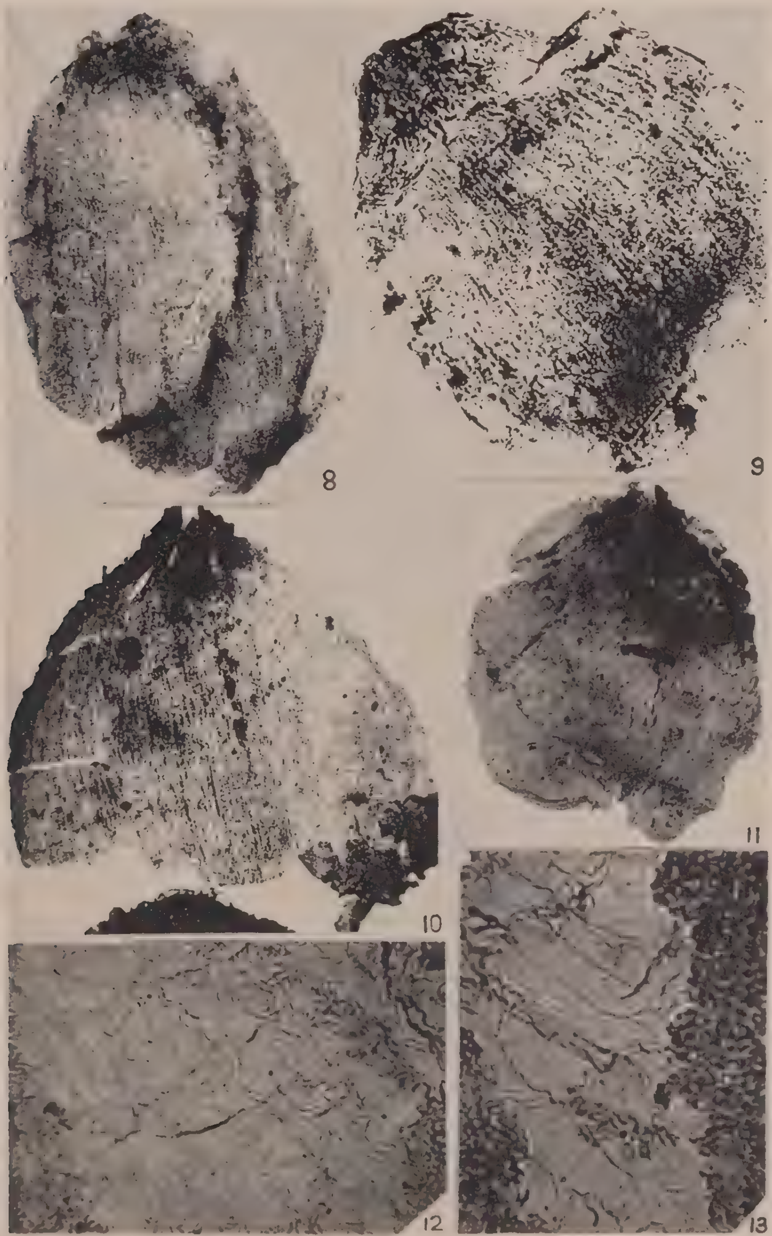
Whenever a Lower Gondwana coal or shale (bearing *Glossopteris*) is analyzed, *Pityosporites* usually appears to be the constant and often dominating feature of the microflora yield, like the species of *Glossopteris* in the coal-bearing Permian and U. Carboniferous megaflora of the southern hemisphere (Virkki, 1945; Ghosh and Sen, 1948; Sen, 1948, 1953). In the eastern part of the Ranigunj coalfield the frequency of occurrence of *Pityosporites* in successive higher beds has been found to be closely related to the vertical distribution of the number of species of *Glossopteris* occurring in the Ranigunj stage. Virkki (1945) also obtained a few *Pityosporites* adhering to small pieces of cuticle of *Glossopteris browniana* from a macerated piece of shale from the Permocarboniferous rocks of Newcastle, New South Wales. It may not be very wise to underrate such a close association of *Pityosporites* and *Glossopteris* existing over a great length of time and spread over an extensive area. In the history of palaeobotany detached organs have often been assumed to be related parts on grounds of close association in the same bed. The author feels that the claim of *Pityosporites* being the pollen belonging to *Glossopteris* is a sound proposal like many others have before. If *Pityosporites* is finally accepted as the pollen of *Glossopteris*, it is logical to conclude that the structures bearing *Pityosporites* are microsporangia of *Glossopteris*.

Schopf *et al.* (1944) hold that there can be little doubt about grains of the *Pityosporites* type being referable to Coniferae. This assumption is entirely based on superficial similarities of the *Pityosporites* type of grain with those of modern Abietineae. These authors did not refer to any possible organic or geological association of *Pityosporites* with such palaeozoic conifers. At the same time they recognized the diversities of forms included in *Pityosporites* which, in their opinion, contains probably elements of separate families. "Florin (1940) considers *Pityosporites* to be a completely artificial genus which has no type species". This is apparently true in view of the fact that a wide variety of two-winged spores is included in the genus *Pityosporites*. Such an artificial and heterogeneous genus as *Pityosporites* should be broken into more natural units. Kosanke (1950) has already taken a step in this direction.

EXPLANATION OF FIGURES

FIGS. 8–13. Microsporangia containing or associated with *Pityosporites* sp. FIG. 8. A sporangium showing the nature of characteristic apical dehiscence. Note the base of the sporangium and the texture of its wall. x 55. FIG. 9. An undehisced slightly carbonised sporangium. Note the nature of the apical portion, and the texture of the sporangium wall. x 55. FIG. 10. A sporangium found in association with an irregularly compact mass of *Pityosporites*. Note the texture of the wall. x 50. FIG. 11. A thin membranous shrunk remnant of a sporangium-like body showing circular dehiscence at one end. Note the partial carbonisation of the dehisced portion. x 55. FIGS. 12 and 13. Note regularly and/or irregularly rectangular cells of the sporangia with sinuous or straight cell walls. The former type of cell wall is predominantly present in the sporangia walls, the latter type is usually characteristic of the base and/or apex of some sporangia. Note also the disorganized mass of cells in both the figures. x 280.

It is certain that not all spores so far referred to *Pityosporites* reported from the *Glossopteris* rich Lower Gondwana rocks of the southern hemisphere are different from those occurring elsewhere.



Moreover, the coniferous affinity of *Pityosporites* is solely based on a theoretical assumption. Under these circumstances the sporangia containing typical Gondwana *Pityosporites* appear to be referable to *Glossopteris* despite the former's hypothetical relationship to conifers. The short discussion of the botanical affinities of *Glossopteris* that follows is based on this assumption.

AFFINITIES OF THE Glossopteris

Glossopteris fronds are often found in association with small seeds (Walton, 1940) and *Vertebraria* stems possessing secondary wood with multiseriate bordered pitted tracheids and parenchymatous medullary rays of gymnospermous type (Walton and Wilson, 1932). It is now known that most probably *Glossopteris* and *Vertiebraria* are not parts of the same plant (Thomas, 1952a). But the recent discovery by Plumstead (1952) of extraordinary types of ovulate organs found attached to some species of *Glossopteris* has finally established the fact that these plants are really spermatophytes. Unfortunately, no known pollen sac type is referable to *Glossopteris*.

The simple unilocular sporangia containing *Pityosporites* described in this paper appear to be akin to those of primitive gymnosperms. The pollen of these sporangia, i.e., *Pityosporites*, superficially resemble those of Abietaceae as suggested by Schopf *et al.* (1944), but it is quite improbable that *Glossopteris* represents leaves of a conifer. Moreover the pollen sacs studied by the author are not abietinean.

The ovulate organ described by Plumstead (1952) is unique. Being a frond "it may be regarded as a pteridosperm, if that term is used in a very broad sense; but it differs from all the known plants of this type in both vegetative and reproductive characters" (Thomas, 1952b). Harris (1952) too was reluctant about including it in pteridosperms, for Plumstead's (1952) interpretation of the ovulate organ of the *Lanceolatus* type suggests that this plant could also be an angiosperm.

An assemblage of detached organs consisting of *Glossopteris* fronds, simple microsporangia of the kind described in this paper, and cupular organs protecting seeds, as found attached to *Glossopteris* by Plumstead (1952), apparently can not be referred to any known group of plants. "The present author is inclined to follow the suggestions forwarded by Edwards (1952) that the genus belongs to some unknown or imperfectly known group of gymnosperms" (Sen 1955).

SUMMARY

Some microsporangia associated with *Pityosporites* type of pollen were recovered from Indian Lower Gondwana coal. Because of their close association throughout the Lower Gondwanas several types of *Pityosporites* have long been regarded as pollen of *Glossopteris*. Consequently the structures containing them are microsporangia referable to *Glossopteris*. In the past microsporangial structures belonging to *Glossopteris* were recorded with some uncertainty.

The affinities of *Glossopteris* and *Pityosporites* are discussed.

I am indebted to Professor Tom M. Harris, F.R.S., Reading University, U.K., for his valuable criticism of the manuscript.

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Morphologic Variation in Puccinia menthae[1]

John W. Baxter
(*University of Wisconsin—Milwaukee, Milwaukee, Wis.*)

The mint rust fungus, *Puccinia menthae* Pers., is an autoecious, long-cycle rust occurring on a large number of genera of the family Labiatae throughout the world. Morphologic variation within this species has long been recognized. Fischer (4) pointed out that in European forms occurring on *Mentha longifolia* Huds., *Mentha arvensis* L., and *Origanum vulgare* L. the teliospore wall is dark, with small, inconspicuous tubercles, while in the forms on *Satureja vulgaris* L., *Calamintha officinalis* Moench., and *Mentha aquatica* L. the wall is paler and more coarsely verrucose. Cruchet (2), in studying physiologic specialization in the mint rust fungus, observed morphologic differences among specialized races. These were chiefly variations in the color and sculpturing of the telio-spore wall. The occurrence of morphologic variation among European forms of *P. menthae* was also pointed out by Sydow (6).

In many specimens of *P. menthae* from North America the teliospores are larger and more coarsely verrucose than are those of European specimens. The forms occurring on *Monardella* and *Satureja* in the western United States were considered by Dudley and Thompson (3) to be sufficiently distinct to deserve specific rank. The two species which they described, *Puccinia monardellae* Dudl. & Thomp. and *Puccinia micromeriae* Dudl. & Thomp., were later reduced to synonymy with *P. menthae* by Arthur (1). In discussing the variability of the mint rust fungus in North America, Arthur pointed out that the telio-spores from western specimens tend to be larger, thicker-walled and more strongly sculptured than those of collections from eastern North America.

This paper presents the results of a study of morphologic variation within *P. menthae* in Europe and North and South America. Four varieties are established herein on the basis of the color, thickness and sculpturing of the teliospore wall, the nature of the pedicel and, to some extent, size of teliospores. Several variant forms within varieties are recognized. In view of the intergradation among these forms it does not seem advisable to describe them as distinct taxa.

Puccinia menthae Pers., Syn. Meth. Fung. 220. 1801, var. menthae. (Fig. 1).

Uredo menthae Pers., Syn. Meth. Fung. 220. 1801.
Dicaeoma menthae S. F. Gray, Nat. Arr. Brit. Pl. **1:** 542. 1821.
Puccinia pycnanthemi Schw., Trans. Am. Phil. Soc. **2:** 295. 1832.
Puccinia menthae (Pers.) var. *americana* Peck, 25th Rept. N. Y. St. Mus. 115. 1872.

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Puccinia micromeriae Dudl. & Thomp., Jour. Mycol. **10:** 54. 1904.
Dicaeoma micromeriae Dudl. & Thomp. Arth., N. Am. Flora **7:** 406. 1921.

Teliospores 16–25 x 19–32 μ, wall 1–3 μ thick, cinnamon- or chestnut-brown, verrucose-echinulate or obscurely verrucose; pedicel 70 μ or less

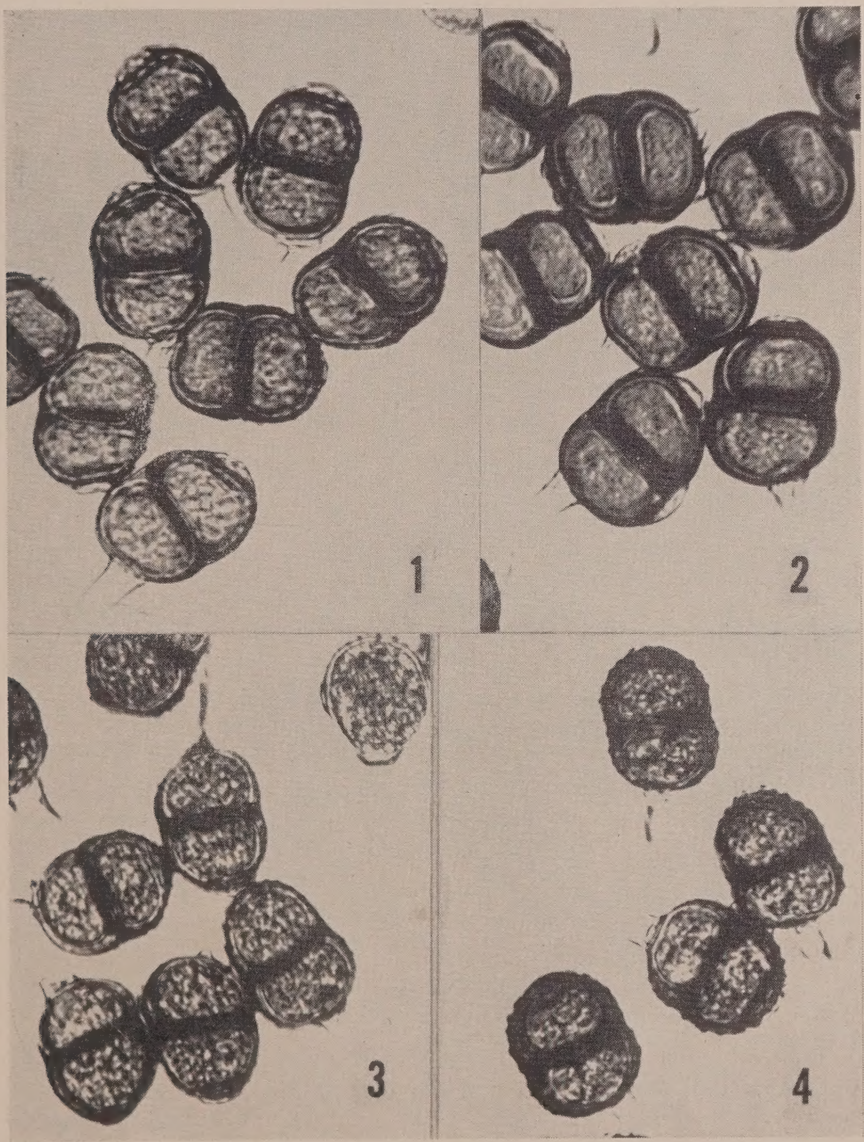

FIG. 1. Teliospores of *Puccinia menthae* var. *menthae*. (From type.) X 800. FIG. 2. Teliospores of *P. menthae* var. *menthae*, variant I. X 800. FIG. 3. Teliospores and urediospore of *P. menthae* var. *menthae*, variant II. X 800. FIG. 4. Teliospores of *P. menthae* var. *menthae*, variant IV. X 800.

in length, usually smooth-walled, occasionally roughened in the lower portion.

TYPE SPECIMEN: On *Mentha* sp., Persoon (no date or locality).

HOSTS AND DISTRIBUTION: Worldwide, on species of *Mentha*, *Monarda*, *Blephilia*, *Cunila*, *Pycnanthemum*, *Satureja*, *Hedeoma*, *Origanum*, *Lycopus*, *Melissa* and *Thymus*.

The type cited above is the lectotype selected by Jϕrstad (5) in a recent revision of Persoon's types in the Rijksherbarium, Leiden.

Four intergrading variant forms of *P. menthae* var. *menthae* occur in North America. The chief characteristics and approximate host range of these variants are presented here.

Variant I. (Fig. 2.) Teliospores 18–25 x 24–32 μ; wall 1–3 μ, dark chestnut-brown, obscurely verrucose, frequently appearing smooth; pedicel 30–70 μ.

Hosts and distribution: *Mentha piperita* L., Oregon, Washington.

Variant II. (Fig. 3). Telia chestnut-brown; teliospores 16–22 x 19–28 μ; wall 1–2 μ, cinnamon-brown, verrucose-echinulate; pedicel deciduous or occasionally persistent and up to 35 μ long.

Hosts and distribution: *Pycnanthemum pilosum* Nutt., Illinois, Indiana, Iowa, Kansas, Missouri, West Virginia; *Mentha spicata* L., Pennsylvania, Indiana.

Variant III. Teliospores 20–23 x 23–30 μ; wall 1.5–3 μ, chestnut-brown, coarsely verrucose-echinulate; pedicel up to 70 μ long, occasionally rugose and slightly inflated in the lower one-third.

Hosts and distribution: *Mentha arvensis* L., North America, from Iowa westward; *Monarda fistulosa* L., Indiana westward to Nebraska.

Variant IV. (Fig. 4). Teliospores 20–23 x 26–30 μ; wall 1.5–3 μ, chestnut-brown, coarsely verrucose-echinulate; pedicel 30–60 μ long.

Hosts and distribution: *Satureja vulgaris*, eastern North America.

PUCCINIA MENTHAE Pers. var. **cordillerensis** var. nov.

Puccinia monardellae Dudl. & Thomp., Jour. Mycol. **10:** 53. 1904.
Dicaeoma monardellae (Dudl. & Thomp.) Arth., N. Am. Flora **7:** 406. 1921.

A forma typica speciei differt teliosporis 20–27 x 23–40 μ, membrana 2–4 μ cr., intense castaneo-brunnea, verrucoso-echinulata vel verrucoso-aculeata; pedicello 60–120 μ longo, deorsum rugoso, frequenter lenissime incrassato.

Teliospores 20–27 x 23–40 μ, wall 2–4 μ thick, dark chestnut-brown, verrucose-echinulate to verrucose-aculeate; pedicel 60–120 μ long, rugose in the lower portion, frequently slightly inflated.

TYPE SPECIMEN: On *Monardella macrantha* Gray, San Bernardino, Calif., July 8, 1898, S. B. Parish; Barth. N. Am. Ured. 753 (as *Puccinia monardellae*).

This variety occurs on species of *Monardella*, *Monarda*, and *Hedeoma* in western North America and on *Bystropogon* spp. and *Satureja parvifolia* (Phil.) Epling in western South America. Although its range overlaps that of variety *menthae* in western North America it appears to be limited to the western mountainous region and the plains states. It shows considerable variation in teliospore morphology and can be divided into the following intergrading forms:

Typical Form. (Fig. 5). Teliospores 22–27 x 28–40 μ, wall 2–4 μ, thickened to 5–6 μ at the apex, dark chestnut-brown, verrucose-aculeate; pedicel 90–120 μ long, rugose and inflated in the lower portion.

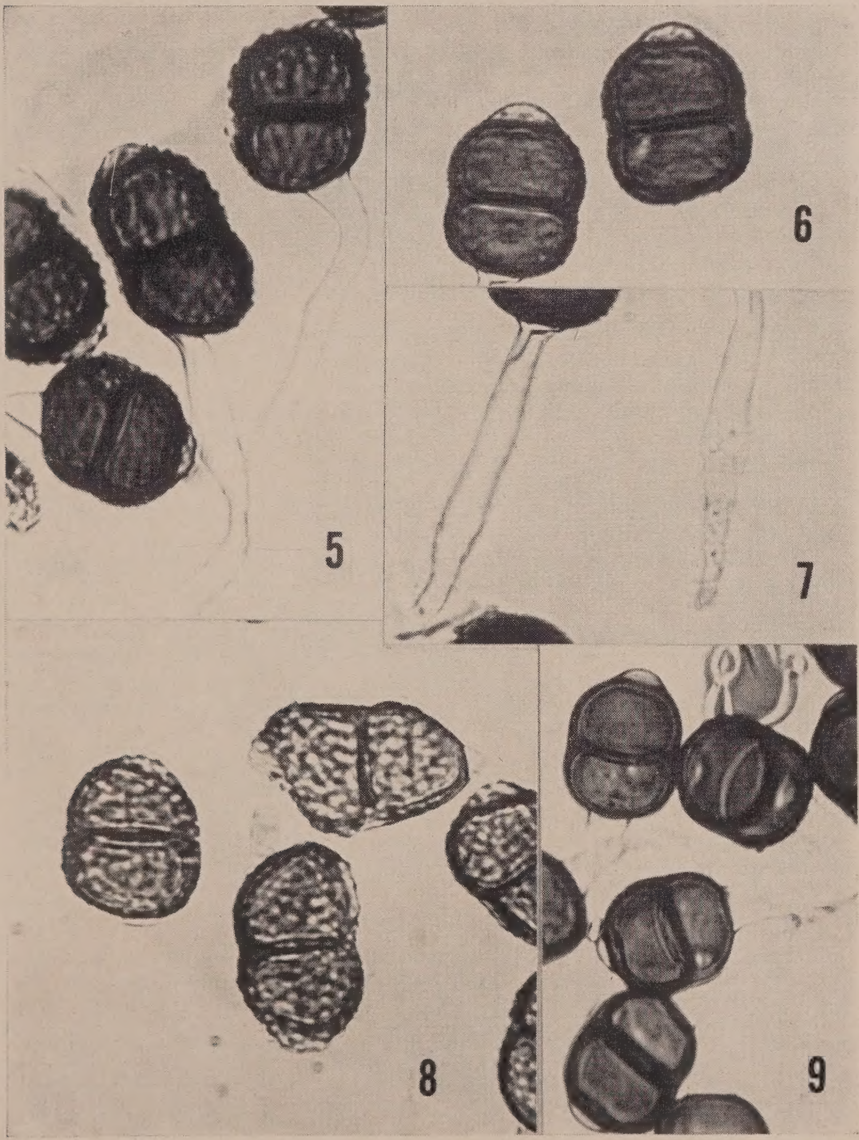

FIG. 5. Teliospores of *P. menthae* var. *cordillerensis*. (From type.) X 800. FIG. 6. Teliospores of *P. menthae* var. *cordillerensis*, variant III. X 800. FIG. 7. Teliospore pedicels of *P. menthae* var. *cordillerensis*, variant III. X 800. FIG. 8. Teliospores of *P. menthae* var. *rugosa*. (From type.) X 800. FIG. 9. Teliospores of *P. menthae* var. *levis*. (From type.) X 800.

Hosts and distribution: *Monardella* spp., from the Pacific coast eastward to Utah, Colorado and New Mexico.

Variant I. Teliospores 22–24 x 26–32 μ, wall 2–3 μ, dark chestnut-brown, verrucose-echinulate to verrucose-aculeate; pedicel up to 100 μ long, rugose and inflated in the lower portion.

Hosts and distribution: Species of *Monarda* and *Hedeoma* from the plains states westward.

Variant II. Teliospores 20–24 x 23–30 μ; wall 2–3 μ, dark chestnut-brown, verrucose-aculeate; pedicel 60–80 μ long, lower portion rugose and somewhat inflated.

Hosts and distribution: *Satureja parvifolia*, Argentina.

Variant III. (Figs. 6, 7). Teliospores 22–26 x 26–40 μ, wall 2–3 μ, dark chestnut-brown, verrucose-echinulate; pedicel 60–80 μ long, lower portion rugose and inflated.

Hosts and distribution: *Bystropogon* spp., Peru, Bolivia.

PUCCINIA MENTHAE Pers. var. **rugosa** var. nov. (Fig. 8).

A forma typica speciei differt teliosporis 22–26 x 27–38 μ; membrana 2–3 μ cr., rugoso vel rugoso-aculeata.

Teliospores 22–26 x 27–38 μ; wall 2–3 μ thick, cinnamon-brown or pale chestnut-brown, rugose to rugose-aculeate; pedicel deciduous or occasionally persistent, 30 μ or less in length.

TYPE SPECIMEN: On *Bystropogon mollis* H.B.K., Cuenca, Ecuador, Sept. 10, 1920, Holway 978.

The rugose sculpturing of the teliospore wall in this species is unlike that of any other form of *P. menthae*.

PUCCINIA MENTHAE Pers. var. **levis** var. nov. (Fig. 9).

A forma typica speciei differt teliosporis 19–20 x 19–26 μ, membrana 1.5–3 μ cr., intense castaneo-brunnea, levi; pedicello 60–90 μ longo.

Teliospores 19–20 x 19–26 μ, wall 1.5–3 μ, dark chestnut-brown, smooth; pedicel 60–90 μ long.

Type specimen: On *Satureja odora* (Gris.) Epling, San Javier, Cordoba, Argentina, Sept. 5, 1949, Leal 12474.

This variety differs from all other forms of *P. menthae* in having smooth-walled teliospores. Examination of teliospores in a dry mount and under oil immersion reveals no evidence of sculpturing.

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